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# Timing Performance Error in Rewarded and Non-Rewarded Tasks

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by

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Abstract

The literature on human and nonhuman animal interval timing disagrees about whether perceived time is a linear or power function of real time, and to what extent reward influences timing performance. Two competing computational learning and timing models, Temporal Difference (TD, Schultz, 2013) and Sometimes Competing Retrieval (SOCR, Stout & Miller, 2007) are reviewed. The present experiments investigate human interval timing error in both reward and non-reward conditions. The experiments were simulated by a computational model to identify both the function that describes the effect of interval duration on the distribution of variance (e.g., scalar or linear) and the relative predictive power of the SOCR and TD models, and the effects of reward on interval timing. Specifically, it was hypothesized that 1) timing variability is scalar, not linear, 2) that a modified SOCR model explains the data, and 3) that interval timing performance is less variable in rewarding situations than in non-rewarding situations. Timing trials involved the presentation of a reference duration; participants then produced their estimate of that duration while under cognitive load (random number generation and serial math tasks) through key presses on a computer. The results failed to support these hypotheses. However, reward produced a nonsignificant tendency towards early responding. Finally, suggestions for further research, including further computational modeling and investigation of the neural substrata of reward and timing are discussed.

Keywords

Learning, Reward, Computational Modeling, SOCR, RTCM, Scalar Timing, Psychophysics, Human Timing Error

Timing Performance Error in Rewarded and Non-Rewarded Tasks

## Introduction

The ability to accurately judge the passage of time is important for all human and non-human animals. Well-timed sequences of behaviors allow animals to prepare for motivationally relevant stimuli such food or predators (Silva & Timberlake, 1999; Timberlake, 1997). Thus, timing is important for survival, particularly in the coordination of predatory and escape movements, in foraging (e.g., estimating when to return to previously-exploited feeding grounds), and in estimation of mating seasons. Overall, these well-timed behaviors depend critically on accurate predictions, a critical function of reward-based learning (Allan, 1998; Kacelnik & Brunner, 2002; Malapani & Fairhurst, 2002). Thus, timing is evolutionarily adaptive and is essential for survival. Many species, including modern humans (even without clocks), can produce endogenous circadian rhythms that match the length of a solar day within ± 1% accuracy, though the judgment accuracy of second- and minute-long timescale intervals is relatively poor, ranging from 40% to 95% accuracy in many species (Malapani & Fairhurst, 2002). Empirical and theoretical analyses of timing systems are important because timing is evolutionarily functional, for example, in allowing animals to learn temporal connections between stimuli predictive of food and the occurrence of food (e.g., Bolles, 1972).

The circadian rhythm is controlled by the suprachiasmatic nuclei (SCN), which is informed in large part by cyclic daily solar input (Schroeder & Colwell, 2013; Partch, Green, & Takahashi, 2014). SCN function has been described in molecular, genetic, and neurophysiological terms in *Drosophila* fruit flies, with data on SCN function in mice and humans suggesting similar function across species (Hinton & Meck, 1997; Partch et al., 2014). However, evidence suggests that the SCN is not responsible for ‘timekeeping’ in seconds or

minutes long time scales (‘interval timing’). Specifically, SCN lesions reduce or eliminate circadian rhythmicity in rodents. However, ten-second interval estimation tasks were seemingly unaffected by these SCN lesions (Lewis, Miall, Daan, & Kacelnik, 2003). Thus, different brain systems seem to contribute to interval timing in long and short time scales. The SCN allows for timing across relatively long (circadian) durations while other systems, including the midbrain dopamine (Matell & Meck, 2004) and cerebellar systems, operate on much shorter intervals (i.e., seconds and minutes).

Evidence from human participants suggests interval timing is driven by dopaminergic neurons in the substantia nigra pars compacta (SNc), providing a neural ‘pacemaker’ with irregular pulses occurring approximately every 200 ms (Matell & Meck, 2004; Hinton & Meck, 2004). These pacemaker neurons work in concert with frontal and striatal regions comprising a distributed neural interval timing circuit, *inter alia*, providing input to other regions (e.g. hippocampus) that enable associative learning (Matell & Meck, 2004).

A full description of interval timing neural circuitry is hampered by the sheer number of neurons involved (Hinton & Meck, 1997; Hinton & Meck, 2004). In associative learning situations, computational modeling is used to mathematically simulate the operation of such systems. Improved fits to empirical data suggest greater confidence that the model mimics true neural network operation (Arantes, 2008; Gibbon, 1977; Malapani & Fairhurst, 2002). Arguably, Rescorla and Wagner’s (1972) model is the most successful in explaining associative learning phenomena. Their model assumes that learning depends on (1) the contiguity between an antecedent cue (e.g., a conditioned stimulus [CS]) and an outcome (e.g., an unconditioned stimulus [US]) and (2) the surprisingness of the outcome. Thus, contiguity and surprise are conjointly necessary and sufficient for learning. Mathematically, learning is modeled by:

$$\Delta V_{X-US} = \alpha_X * \beta_{US} (\lambda_{US} - \Sigma V_{i-US}) \quad \textit{(Equation 1)}$$

where $\Delta V_{X-US}$ is change in the associative value of $V_{X-US}$ after each trial, $V_{i-US}$ is the expectation of an unconditioned stimulus (US) presentation, $\lambda_{US}$ is the actual occurrence of the US, and $\alpha_X$ and $\beta_{US}$ are US and target stimulus (X) saliences, respectively. As an animal experiences repeated CS – US pairings, the value of $\lambda_{US} - V_{i-US}$ decreases as expectations more closely match actual occurrence of stimuli (Rescorla & Wagner, 1972; see Table 1 for full equations). Rescorla and Wagner's (1972) model explains many basic learning phenomena (e.g., Kamin's [1968] blocking), but it fails to explain human and nonhuman animal timing variability in interval timing tasks. In contrast to empirical data, this model parses time into trial-sized bins and, consequently, is silent concerning the variations in learning and performance that might occur within a trial. Additionally, the model is silent concerning variability in interval timing tasks.

Gibbon's (1977) Scalar Expectancy Theory (SET) model is among the most widely cited computational models of interval timing. SET suggests that a pacemaker-accumulator-comparator system operates in conjunction with working memory. Here, the pacemaker generates rhythmic pulses (about 5 Hz, Matell & Meck, 2004) that are stored in the accumulator, where these timing pulses are counted, or 'accumulated'. The accumulator feeds these counted pulses to both the comparator and to memory. Memory stores these counts from multiple trials in a learning task, feeding this information to the comparator. The comparator is believed to make timing decisions based on the similarity of ratios between accumulator and memory inputs (Arantes, 2008; Gibbon, 1977; Machado & Arantes, 2006). The 'scalar' in SET refers to the scaled (being multiplied by a constant) temporal distribution of behavioral variance in learning tasks. That is, SET makes important assumptions concerning the psychophysics of time perception.

From SET, two parameters describe the psychophysical relationship between the actual and perceived duration of the reference interval: the coefficient of variation (described by Weber's Law) and the psychophysical exponent (described by Steven's power law). Weber's Law describes the relationship between the standard deviation of interval estimates and mean perceived time. That is, the standard deviation of interval estimates is a constant fraction of the mean duration of the estimated interval (Allan, 1998). Specifically, Gibbon (1977) observed so-called scalar variation in perceived time, which follows the generalized formulation of Weber's law:

$$\text{Coefficient of Variation (CV)} = \frac{\sigma}{t} \qquad \textit{(Equation 2)}$$

where σ is the standard deviation of time interval estimates, and *t* is the mean of those time interval estimates (Bizo, Chu, Sanabria, & Killeen, 2006; Wearden, 1991). Indeed, one of the primary ways to test for empirical scalar timing is to show that the coefficient of variation is nearly equal for all experimental durations (Wearden & Lejeune, 2007).

Weber's Law describes the variability across trials in interval estimation (and reproduction) tasks. In addition, data consistent with Steven's (1961) power law have been observed in multiple learning paradigms using a variety species. That is, there is strong empirical evidence that the empirical relationship between perceived time and real time obeys Stevens' (1961) psychophysical law, which refers to the observation that perception of a stimulus dimension is a power function of the physical value of that dimension. Applied to interval timing tasks, Steven's power law asserts that perceived time is a power function of the duration of the reference interval (see Figure 2), which is captured by the following equation:

$$\Psi = K * \Phi^{\alpha} \qquad \textit{(Equation 3)}$$

where Ψ is the perceived duration of the interval, *K* is a scaling constant, ϕ is the duration of a reference interval, and *a* describes how perceived duration changes as a function of the duration of the reference interval (Billock & Tsou, 2011; Stevens, 1957; Stevens, 1960). The specific value of *a* is unknown and is contentious in the literature, though it is believed to be approximately 0.9, which implies that Ψ is a logarithmic (compressed) function of ϕ. That is, participants in interval estimation (production) consistently underestimate (or underproduce) the duration of the reference interval. To place this in additional context, when *a* equals unity, perceived duration of the interval is a linear function of the reference interval; when *a* is greater than unity, perceived time is an exponential function of real time; when *a* is less than unity, perceived time is a logarithmic function of the reference interval (Allan, 1998). Empirical scalar timing is observed when the observed mean estimate matches or nearly matches the reference interval (i.e., *a* is near unity) and the coefficient of variation is nearly equal for all reference interval durations (i.e., scalar variability is observed; Wearden & Lejeune, 2008).

Procedures for measuring time perception include both interval estimation and interval reproduction tasks. In interval estimation tasks, participants receive a reference interval and then verbally estimate the duration of the reference interval. In example, a cue may be presented, followed the phrase ‘wait’ presented on screen, then another cue identical to the first. Participants are then asked to estimate how long the ‘wait’ interval was (e.g. Martin, Poirier, & Bowler, 2010). In interval reproduction tasks, participants receive a reference interval and then reproduce the duration of the reference interval through behavioral tasks. For example, subjects might produce lever presses indicating the beginning and end of that reproduction of the interval, or may be presented with a visual stimulus for a given amount of time, and afterwards attempt to

reproduce that time duration through holding down a keyboard spacebar for as long as they believe that stimulus was presented on the screen (Pandle, Shindley, Parganiha, & Pati, 2013).

One important difference between time interval estimation and reproduction tasks is that estimation tasks involve perception while reproduction tasks involve both perception and motor performance (Pastor, Artieda, Jahanshahi, & Obeso, 1992). Animal studies investigating linear and SET timing variance (e.g. Bizo et al., 2006) are conducted using estimation tasks (though these tasks have a motor component, for example, shifting from pressing one lever to another in temporal bisection tasks), while human participants may perform either task type. The present work uses time reproduction tasks as only three reference intervals were used (5, 15, 25 s) and it was believed participants would find it too easy to distinguish between durations, leading to less variability than in a reproduction task. As this study seeks in investigate timing variation, estimation tasks possibly limiting that variation were avoided.

Interval reproduction and estimation studies across multiple species, including humans, rats, mice, pigeons, and fish (Bizo et al., 2006; Drew, Cooke, Zupan, Couvillon, & Balsam, 2005; Wearden, 1991; Wearden, 2013), have supported SET. Here, subjects tasked with estimating or reproducing a time interval demonstrate mean time estimation generally very close to, though short of, the actual interval, with only a few documented systematic differences between mean time estimation and the actual length of an interval. This implies that the value of *a* is near unity. However, as the duration of the interval to be estimated increases, the standard deviation ($\sigma$) of time interval estimation tends to increase (Kacelnik & Brunner, 2002; Malapani & Fairhurst, 2002).The nature of this tendency is not fully understood, and is contentious in the literature (Allan, 1998; Bizo et al., 2006; Killeen, 2014). Previous research has indicated that the CV of time estimation variability is about 0.3 (Rakitin, et al., 1998). However, many variables

can influence the specific CV value, including the nature of the task (interval estimation vs. production).

Though many laboratories have presented findings indicating that time perception is a power function of real time ($a \approx 0.9$), a sizeable minority suggest that it is linear ($a = 1$). Allan (1998) noted that most data suggest that the perceived duration of an interval is a linear function of the reference interval (i.e., $a = 1$), and that logarithmic relationships are found only with well-trained subjects or participants. This statement, however, remains contentious, and the true value of the exponent (see Equation 3) remains open for debate and further investigation (Allan, 1998; Bizo et al., 2006; Galtress, Marshall, & Kirkpatrick, 2012).

Seeking evidence for scalar variability (see Equation 2), Bizo et al. (2006) trained 12 pigeons to peck two keys for food reward while performing a time estimation task. In this experiment, pigeons were provided with a reference time interval (light 'on' duration). Pecking one key resulted in food reward only when pecked before the reference time interval elapsed; the other key resulted in food reward only after the time reference interval elapsed. However, to avoid satiation before the interval elapsed, each key would provide reinforcement on only one-half of valid pecks. Time interval estimation was assessed as the point at which the pigeon shifted from pecking the 'under limit' key to the 'over limit' key. In total, birds received 100 trials at 1, 2, 4, 8, 6, 32, and 64 seconds. In contrast to their expected results, Bizo et al.'s data were inconsistent with observations of scalar variability. That is, a larger CVs (Equation 2) were observed for longer time estimation intervals.

Bangert, Reuter-Lorenz, & Seidler (2011) investigated scalar variability in three experiments with human participants. In the first experiment, participants received two 50-ms auditory cues followed by a silent reference interval of 300, 650, 1000, 1350, or 1700 ms, which

was, in turn, followed by another pair of 50-ms tones. Participants attempted to reproduce the reference time interval between the pairs of tones by tapping the space bar of a computer keyboard twice, thereby indicating the start and stop of their time interval reproductions. During the first few trials, participants received visual feedback on a computer screen indicating their accuracy in the reproduction of the reference time interval. As in Bizo et al.'s (2006) study, Bangert et al. (2011) failed to observe scalar variability. However, Bangert et al. (2011) note that the CVs were nearly equal for durations up to approximately one second, but not for durations longer than one second. That is, the standard deviation in the 300, 650, and 1000 ms conditions increases at a linear rate. Resultantly, these investigators propose that a shift from linear to logarithmic processing occurs at about the one-second point in time estimation tasks, though they neglect to provide the specific value for their exponent.

As noted, the neural mechanisms of interval timing are not fully elucidated, though are thought to be driven in large part by the oscillatory activity of dopaminergic neurons in the SNc. DA signals drive cortico-striatal-thalamic timing circuitry in the dorsal striatum (DS), globus pallidus, thalamus, prefrontal cortex (PFC), and cortical motor regions. As shown in Figure 3, neural systems involved in decision making overlap partially with these timing circuits, with PFC, thalamus, and the basal ganglia (including DS) being involved in both timing and decision making. Furthermore, neural systems involved in reward prediction show significant overlap with timing and decision making circuitry. In particular, PFC, SNc, and basal ganglia are involved in timing, decision making, and reward prediction (Galtress et al., 2012; Kirkpatrick, 2014; Wearden, 2013).

Malapani and Fairhurst (2002) reviewed evidence suggesting time interval estimation utilizes scalar functions in both human and non-human animals. Moreover, they reported that

Parkinson's disease (PD) patients are impaired in time estimation (higher CVs while off medication) and that a therapeutic DA agonist reduces this impairment. PD is associated with reduced DA activity, particularly in nigrostriatal circuits (SNc to basal ganglia), a deficit that is partially corrected with dopamine-agonist medication. Other investigators have reported similar results for several within-subjects experiments in which PD patients on and off medication estimated and reproduce intervals ranging from 250 to 2000 ms in duration. These patients also demonstrated less variability in these tasks while on medication relative to when off medication (Jones, Malone, Dirnberger, Edwards, & Jahanshahi, 2008). While PD does involve motor disability, Pastor et al. (1992) have shown the time reproduction tasks in PD patients are not merely a function of this motor disability (i.e. they also involve perceptual distortion).

Schultz's (2013) temporal difference (TD) model assumes that the neural processing of a reward, or of an absent-but-expected reward, is driven by DA-ergic systems behaving in accordance with the following mathematical rule:

$$\text{DA Response} = \text{Actual Reward} - \text{Predicted Reward} \qquad \textit{(Equation 4)}$$

Accordingly, DA Response encodes the unexpectedness of the reward (i.e., prediction error). For example, if an unexpected reward is received, dopamine activity increases, as does salience to stimuli associated with that reward. When a reward is predicted but not received, DA-ergic activity pauses. Thus, DA activity is strongly associated with reward processing (Berridge, 2007; Schultz, 2013). Moreover, there is strong suggestion that interval timing variance would be sensitive to the value of the reward because timing is both driven by DA and is believed to influence reward processing (Allan, 1998; Kacelnik & Brunner, 2002; Malapani & Fairhurst, 2002).

DA release in the nucleus accumbens (NAc) is triggered by exposure to reward and seems to be critically involved in reward learning (Berridge, 2012; Berridge & Robinson, 1998; Schultz, 1998). Variation in DA-ergic activity also affects pacemaker activity and timing task performance. Dopamine agonists such as amphetamine and methamphetamine increase DA activity in NAc, contributing to the reinforcing effects of those drugs through interactions primarily with excitatory $D_1$ receptors (Gnegy, 2012; Haile, 2008). These drugs may also result in increased frequency (faster timing) of DA pacemaker activity (Chiang, et al., 2000; Harper, Bizo, & Peters, 2006). Dopamine antagonists such as haloperidol reduce this frequency, slowing the pacemaker (Buhusi & Meck, 2002; Drew, Fairhurst, Malapani, Horvitz, & Balsam, 2003).

A review of the literature reveals a parallel between the neuropharmacological and cognitive mechanisms of timing. Specifically, DA-ergic function is influenced by reward delivery, reward omission, pharmacological manipulations, and is thought to contribute to timing. At the cognitive level of analysis, the pacemaker component of Gibbon's (1977) SET is influenced by similar variables. Thus, DA activity may be related to the scalar component (specifically, the CV) in SET. Gibbon noted several factors that potentially cause deviations from empirical scalar timing. First, Gibbon suggested that variation in the pacemaker is a source of scalar variability. As discussed above, variation in DA activity affects pacemaker periodicity. Second, variation in the comparator can cause scalar variance (Killeen, 2002). It is suggested that variations in frontal DA activity may affect the comparator (e.g. Galtress et al. 2012). Thus, DA-ergic activity is related to interval timing processes, including scalar variability in timing.

Given the critical role of timing in reward learning and the overlap in neural systems involved in timing, reward prediction, and decision making, timing may be investigated through the use of reward prediction or decision making tasks. Much of the previous work on interval

timing has utilized such an approach (Galtress et al., 2012; Kirkpatrick, 2014; Wearden, 2013). Additionally, timing may be assessed through computational methods (Galtress et al., 2012). Computational models of timing that accurately predict the results of timing experiments can potentially illuminate the neural circuits contributing to timing – identifying the cognitive processes and mechanisms of timing circuit allows for increased understanding of the computational roles of neural systems involved in timing. As an example, theoretical work with neural networks led to the development of theories that long-term potentiation is the neural basis of memory (Martinez, Jr. & Derrick, 1996). The present study shall build on both the operational and computational foundations laid by previous investigators.

Much of the timing literature involves investigations of timing tasks in the millisecond or second timescales (Arantes, 2008; Cerutti, Jozefowiez, & Staddon, 2013; Drew et al., 2005; Kacelnik & Brunner, 2002). Importantly, this affords the investigator opportunity to build upon previous timing studies, to design and implement improved timing tasks, and in these time scales, to assess the results of such studies through computational modeling. Finally, computational models can be utilized to predict the results of real world studies. It is suggested that the models more accurately predicting real world results (relative to competing models) have stronger validity and value.

Procedural differences among experiments complicate interpretation of the interval timing literature. For example, beginnings and ends of reference intervals are indicated by cues from different sensory modalities (e.g. Bangert et al., 2011; Bizo et al., 2006), which could produce differences in interval timing task performance (Lustig and Meck, 2011). Further, older humans may react more quickly (or slowly) to a cue presented in a given sensory modality

relative to younger individuals. Unfortunately, similar data are not available for nonhuman animal subjects. This precludes some between-experiment comparisons.

Another central problem involves the choice of computational model used to explain interval timing processes in reward learning paradigms. As discussed, the Rescorla and Wagner (1972) model (RW) is silent concerning timing task variability. Though this model is generally accurate in predicting certain aspects of human learning (e.g. associative learning, blocking), it does not address scalar variability in interval timing. Similarly, Schultz's (2013) TD model is an extension of Sutton's (1988) Temporal Difference (TD) machine learning algorithm and Rescorla and Wagner's (1972) model. Unlike RW, the TD model is often described in neurobiological terms, with TD's error term (Equation 3) being comparable to the RW model's treatment of surprise $\lambda_{US} - \Sigma V_{i-US}$ (Equation 1).

The TD model assumes that animals process stimuli in real time instead of trial-by-trial. Nonetheless, like RW, TD assumes that processing is based on all present stimuli (Schultz, 2013; Sutton, 1988). While TD's error term is supported by neurophysiological evidence (Schultz, 1998; Schultz, 2007; Schultz, 2013), it too fails to explain the scalar timing variability observed in many interval timing experiments (e.g. Gibbon, 1977; Malapani & Fairhurst, 2002; Wearden, 1991). Additionally, the TD and RW models suggest that scalar variation in a human or nonhuman animal's performance is based in a failure to learn cues. Alternately, it may be that poor performance on a task is based in failure at the performance stage, not during learning.

In learning psychology, the relative (rather than the absolute) value of a conditioned stimulus (Miller & Matzel, 1988) or a reinforcer controls behavior. For example, in behavioral contrast experiments, a high-value reinforcer (e.g., 5 food pellets) is more effective after an animal has experience with a low-value reinforcer (e.g., 1 food pellet) than after experience with

only the high-value reinforcer. That is, animals learn and respond based on the relative value of a reward. Similar results have been observed in a variety of learning situations. This is problematic for (or at least outside of the scope of) the TD model. This is particularly relevant when the relative values of multiple cues are different. The Sometimes Competing Retrieval model (SOCR, Stout & Miller, 2007) emphasizes the relative value of cues and is thus expected to be more predictive of human and nonhuman animal interval timing variability (see Table 1 for SOCR equations).

Specifically, unlike competing models (e.g. RW and TD), Stout and Miller's (2007) SOCR model rejects the view that multiple cues compete for associative strength with an outcome. Instead, it assumes that cue competition effects such as blocking are driven by processes that occur at the time of retrieval. The SOCR model has provided a better fit to empircal data relative to competing models, including RW (Witnauer et al., 2014). SOCR explains many aspects of associative learning with high accuracy relative to other models, suggesting its potential value in describing timing variability in learning tasks. As such, the SOCR model was modified and extended to investigate interval timing variability. This real-time comparator model (RTCM) seeks to predict and explain learning as it occurs within a trial.

RTCM assumes that stimuli are represented by collection of microelements that are activated when a stimulus is presented. The model anticipates well-timed behavior because those microelements show spectral activation and decay (see Figure 4). Here, a real-time variant of Hebb's (1949) contiguity-based learning rule controls changes in associations between microelements. The response strength controlled by a microelement (X) is based on a comparison between the X-outcome association and the representation of the outcome activated by other microelements (i.e., through X-i-outcome associative chains, where i is a microelement

that is associated with X). RTCM's response rule captures the psychological intuition that the response is determined by the value of a predictor (X) relative to other predictors that the animal can retrieve (i) through between-element associations (i.e., the X-i association). See Table 1 for RTCM equations.

In total, the major open issues in the interval timing literature are i) the power vs. linear variability debate (Allan, 1998; Malapani & Fairhurst, 2002), ii) which model of timing provides the best fit to the data, iii) the exact value of the scalar if timing is in fact scalar in nature (Malapani & Fairhurst, 2002), iv) the role of reward in time interval estimation and reproduction (Allan, 1998; Kacelnik & Brunner, 2002), and v) the variation in time interval estimation or reproduction based on cues in different sensory modalities (Lustig & Meck, 2011).

The present studies investigated and addressed the first four of these open issues while holding the fifth item constant. Specifically, it was hypothesized that 1) performance in reproduction of time intervals is a logarithmic and not linear function of the reference interval, 2) RTCM will predict a exponent value of approximately 0.9, and 3), the CV changes based on the presence or absence of reward, leading to shorter time interval reproductions in reward conditions. Two experiments tested these hypotheses; both experiments were conceptually similar in nature, though Experiment 2 sought to improve upon and correct some deficiencies in Experiment 1.

## Experiment 1

The first experiment investigated these hypotheses through a within-subjects design. On each trial, participants were randomly assigned to either a rewarded or non-rewarded condition, with an approximately equal number of trials in each condition occurring over the course of all trials. Over the course of the experiment, participants reproduced the duration of three reference

intervals (5, 15, 25 s). Interval reproduction was indicated by key presses on a computer keyboard indicating the beginning and end of the reproduction. Participants performed a random number generation task during the reproduction period to prevent the 'counting-off' of time.

## Methods

### Participants

Participants included 19 college students fulfilling requirements for research participation credits for an introductory psychology course at SUNY Brockport. Before participating in the experiment, potential participants were asked if they have any visual impairment or any motor difficulties that may prevent them from attending to visual cues or from tapping a computer keyboard key in a timely manner. No potential participants were excluded from the experiment due to these criteria. Participants were advised that the experiment would take approximately 45 to 60 minutes complete. Participants were offered exclusion from the study if they were unwilling to commit to that timeframe, though no participants declined participation. No other measures or exclusionary criteria were used in judging participant qualification to participate in the experiment. Participants then reviewed and signed consent forms.

### Procedure

After signing consent forms, participants were moved into a research cubicle in groups of not more than four individuals. Each participant was seated at a PC. Ten blank pieces of paper (for the random number generation task) and a pen were present at each PC. No clocks were present in the room. Each participant was asked to turn off his or her cell phone, and to submit any wristwatch to the experimenter's care. These procedures were intended to prevent the participant from using any timing device to measure the passage of time during the experiment.

At this time, the experimenter started a PC program (written in PsychoPy 1.76.00; Peirce, 2007; Peirce, 2009) on each of the computers at which a participant was present. The initial screen of the PC program presented the participant with a statement regarding general expectations, a rationale for the study, and advised the participants of their right to quit the experiment at any time. Moreover, basic instructions for the experimental task were provided. See Appendix A for the instructions and debriefing given to participants.

At the beginning of each time interval (5, 15, 25 s, presented in a random order), participants were presented with a visual cue, followed by an on-screen timer counting from 0 seconds up to the current time interval, then a second cue identical to the first. This cue-timer-cue sequence was presented to the participant three times, with instructions indicating that the timer count was the reference time interval for subsequent performance trials.

In a procedure similar to that of Bangert et al. (2011), the participant then moved to the trial phase, being presented with a brief visual cue indicating if the present trial was nonrewarded (though participants are naïve to this meaning). The presence of an alternate visual cue, presented in a manner counterbalanced with nonreward-trial cues, indicated trials in the rewarded condition (see Figure 5). At this point, instructions on the PC screen advised the participant to press the spacebar and begin writing random numbers on the paper provided in the cubicle. Participants were advised to generate as many random numbers as possible on the paper provided during each trial. The participants then pressed the spacebar at the end of each period, thus indicating their reproduction of elapsed time relative to the reference interval.

As the generation of random numbers increases cognitive load (Bains, 2008; Schneider, Joppich, van der Lugt, Dauper, & Munte, 2004), and suppresses counting ability (Jahanshahi, et

al., 1998), this filler task presumably prevented participants from merely ‘counting off’ time, and using that count to estimate time passage.

As this study used a within-subjects design, each trial was either rewarded or nonrewarded, with an approximately equal number of rewarded or nonrewarded trials occurring for each participant over the course of the experiment. At the end of each rewarded trial, the participant earned a small monetary reward ($0.10) based upon the accuracy of their judgment. As money seems to be reinforcing to humans (Bijleveld et al., 2011; Miyapuram et al., 2012), a financial reinforcer was used, and was expected to motivate participants in the reward condition. Specifically, if the response occurred within ± 2.5 s of the reference time interval, the participant received an indication they had earned $0.10. After each successful rewarded trial, money earned for that trial was displayed on the computer screen. After completion of all trials the monetary reward was paid to the participant. The minimum payout was $0.50 and the maximum was $5.00. Participants performing nonrewarded trials received neither monetary reward for that trial nor any other form of feedback between trials.

Each time interval was presented in a random order over 54 total trials. For each participant, the PC recorded the participant ID number, the condition for each trial (reward or nonreward), and for each trial, the lengths of the reference interval period and the participant’s reproduction of that period as recorded by the key presses. After completing the final trial, instructions on the PC screen advised the participant to bring their sheets of random numbers to the experimenter. Participants were then debriefed and paid. The sheets of random numbers were reviewed for any obvious sign of merely counting off time. No such evidence was found.

## Results and Discussion

Data were reviewed and one participant was excluded from analysis due to failure to complete the PsychoPy program. One other participant was excluded from analyses because they 'clicked through' the procedure (defined as three or more reproductions of ≤ 2.0 s in duration). Individual trials were then eliminated if either greater or less than 2 SDs from the mean. After eliminations, remaining data included 83 and 87 trials respectively of reward and nonreward at 5 s, 77 trials each of reward and nonreward at 15 s, and 91 and 94 trials respectively of reward and nonreward at 25 s. Total payouts in the rewarded condition were $7.40 (5 s), $3.80 (15 s), and $3.50 (25 s).

Participants' performance was evaluated in SPSS as a 2 (Reward [reward vs. nonreward]) x 3 (Interval [5, 15, 25 s]) ANOVA. Analyses indicated an effect of duration, $F$ (2, 24) = 354.06, $p < .01$ (see Figure 6), but neither an effect of reward, $F$(1, 25) =.48, $p$ = .50, nor an interaction between reward and interval, $F$ (2, 24) = 0.01, $p$ = .99. Means, standard deviations, and CVs are shown in Table 2. Though neither predicted nor significant, it is interesting to note that in the 5 and 25 s durations the mean reproductions were shorter in the reward condition than in the nonreward condition (see Figure 7). No significant difference in CVs between the reward and nonreward conditions within each interval were found: $F$(1, 8) = .01, $p$ =.91 (5 s); $F$(1, 8) = 1.26, $p$ = .29 (15 s); $F$(1, 10) = .48, $p$ = .51 (25 s). Additionally, as CVs are a function of mean and SD, means and SDs were correlated in both the reward and nonreward conditions, $r$(28) = .70, $p < .01$ (reward), $r$(28) = .74, $p < .01$ (nonreward), and a best-fit linear function was derived through linear regression across all three time intervals, but separately for reward and nonreward. See Figure 8.

An analysis of covariance (ANCOVA) was conducted using the number of random numbers generated during each trial as a covariant. These tests statistically controlled for any differences in the number of random numbers generated on rewarded trials compared to nonrewarded trials. Specifically, this was done to ensure that participants did not generate fewer random numbers on rewarded trials (and perhaps mentally 'counted off' time instead of performing this task). Again, no significant effects were found, *p*s > 0.56.

The first and last four trials in each condition were compared to determine if participants adequately learned the difference between the cues indicating reward vs. nonreward trials. A significant difference was noted in the 15s nonreward condition, $F(1,35) = 4.553$, $p = .04$, with more accurate performance in the last four trials than in the first four trials. This analysis failed to reveal any other significant effects in the other five conditions.

Evaluation of exponents (see Table 5) indicates that hypothesis 1, that performance inaccuracy in reproduction of time intervals is logarithmic and not linear in nature as the duration of those intervals increases, was not supported. Two exponents (reward, nonreward conditions) were fit across all three time durations for each participant that completed trials in each time duration. In the reward condition, M = 1.04, SD = .33, nonreward M = 1.15, SD = .51. Neither best-fit exponent was significantly different from the null hypothesis of 1.00, $t(6) = .31$, $p = .77$ (reward), $t(6) = .76$, $p = .47$ (nonreward), nor were they significantly different from one another, $t(6) = -1.30$, $p = .24$.

Trial data was compared to predictions for both the best-fit linear and exponential functions across all three time durations, but separately for reward and nonreward. The actual mean reproduction time minus the predicted reproduction was computed for all trials. With reward, the exponential function predictions (M = -1.80, SD = 4.40) significantly better fit the

data than did linear function predictions (M = -3.97, SD = 5.51), $t(250) = -8.101$, $p < .01$, though nonreward trials were better fit with the linear function (M = -3.24, SD = 6.86), $t(257) = 8.538$, $p < .01$ than with the exponential function (M = -8.33, SD = 7.26).

Hypothesis 3, that the value of the CV can change based on the presence or absence of reward, was not supported. We expected that reinforced trials would result in smaller standard deviations in interval timing, indicating the effect of a shift in the value of the CV. Only a nonsignificant tendency in the expected direction was observed in all three time intervals. On the other hand, the observed increase in standard deviation with increasing time intervals was not linear. In total, further investigation is needed (see limitations of this study, below).

Experiment 1 had several limitations, including a small number of participants, a limited number of trials (nine each for the six combinations of duration and condition), and a potentially limited opportunity for participants to learn the difference in meaning between the cues indicating rewarded and nonrewarded trials. Based on cash payouts to participants, the latter two of these factors may have factored into performance particularly at the two longer (15s, 25s) intervals. Anecdotal evidence from participants agreed with this interpretation. After the experiment, participants sometimes asked the experimenters if there was any meaning to the two different cues used in the experiment, which suggests that at least some participants did not learn the reinforcement contingencies.

## Experiment 2

Experiment 2 used a procedure similar to that of Experiment 1. Several modifications to the procedure presumably made it easier for participants to learn the difference between cues. Based on the low payouts in Experiment 1, the payout criteria in Experiment 2 was changed to ± 20% (instead of ± 2.5 s). Though this reduced the payout limits for the 5s condition, it was more

liberal in the 15 and 25 s conditions. Additionally, the PsychoPy program in Experiment 2 was modified in order to collect more data; instead of presenting participants with a fixed number of trials, the 5 s duration was looped for 6 minutes, the 15 s condition for 15 minutes, and the 25 s condition for 24 minutes (presented in a counterbalanced order). These loop times, with a 3-s intertrial interval, were intended to provide a roughly equal number of trials for each duration and condition. Lastly, the random number generation task was replaced with a serial math problem task (see Appendix B). Data from 73 participants were eliminated from pilot studies in which the PsychoPy program was modified before arriving at the settings used in Experiment 2. Aggregate data from all 133 participants (including these 73 dropped participants) were evaluated post-hoc, and are discussed in Appendix C.

This second experiment also investigated these hypotheses through a within-subjects design. As in Experiment 1, rewarded and non-rewarded trials were presented in random order, with an approximately equal number of trials in each condition occurring over the course of the experiment. Over all trials, participants reproduced the duration of the three reference intervals (5, 15, 25 s). Time interval reproduction was indicated by key presses on a computer keyboard to indicate the beginning and end of the reproduced interval.

**Participants**

Participants included 41 college students fulfilling requirements for research participation credits for an introductory psychology course at SUNY Brockport. Participants in Experiment 2 were subject to the same initial participation criteria as were those in Experiment 1.

**Procedure**

As above, the procedure for Experiment 2 was identical to that of Experiment 1 with three exceptions: A serial math task replaced the random number generation task, responses were

rewarded if the time estimate was within ± 20% of the reference duration, and the program was looped for 45 minutes instead of repeating for 54 total trials. The math task was intended to prevent participants from using the random number generation task as a means to tally time while also increasing cognitive load (e.g. Ashcraft & Kirk, 2001). Participants were advised to complete as many math problems as possible in one block of problems per trial, then move on to the next block of math problems in the next trial.

## Results and Discussion

Data were reviewed and no participants were excluded from analysis due to their failure to complete the PsychoPy program. Per interval (5, 15, 25 s), participants' data were reviewed, and participant data excluded from analysis if that participant 'clicked through' the study (defined as three or more estimates of ≤ 2.000 s in duration). One participant was eliminated with this criteria. Individual trials were then eliminated if either greater or less than 2 SDs from the mean. After eliminations, remaining data included 550 trials in the 5s reward condition, 545 trials in the 5s nonreward condition, 611 trials in the 15s reward condition, 623 trials in the 15s nonreward condition, 638 trials in the 25s reward condition, and 619 trials in the 25s nonreward condition. Total cash payouts to participants were $32.30 (5s reward), $40.60 (15s reward), and $40.10 (25s reward). As durations were presented in a random and counterbalanced order, in terms of the first, second, and third interval presented to participants, payouts were $35.30 ($1^{st}$), $37.20 ($2^{nd}$), and $40.50 ($3^{rd}$).

As in Experiment 1, participants' performance was evaluated in a 2 (Reward [reward vs. nonreward]) x 3 (Interval [5, 15, 25 s]) ANOVA. Analyses indicated an effect of duration (5, 15, 25 s), $F$ (2, 319) = 4198.61, $p < .01$ (see Figure 9), but no effect of reward, $F$ (1, 320) = 2.06, $p$ =

.15, or effect of interaction between condition and duration, $F$ (2, 320) = 0.44, $p$ = .64. Means, standard deviations, and CVs are shown in Table 3. Though neither predicted nor significant, in the 5 s duration the mean reproductions were shorter in the reward condition than in the nonreward condition (see Figure 10).

No significant difference in CVs between the reward and nonreward conditions within each interval were found: $F$(1, 36) = .24, $p$ =.63 (5 s); $F$(1, 35) = .21, $p$ = .65 (15 s); $F$(1, 35) = .02, $p$ = .89 (25 s). Additionally, as CVs are a function of mean and SD, means and SDs were correlated in both the reward and nonreward conditions, $r$(107) = .65, $p$ < .01 (reward), $r$(107) = .69, $p$ < .01 (nonreward), and a best-fit linear function was derived through linear regression across all three time intervals, but separately for reward and nonreward. See Figure 11.

An analysis of covariance (ANCOVA) was conducted using the number of math problems solved during each trial as a covariant. These tests statistically controlled for any differences in the number of random numbers generated on rewarded trials compared to nonrewarded trials. Though some math task data was unavailable as some participants failed to properly delineate their sets of math problems between trials, no significant effects of the math task, or interactions with either condition or duration were found, all *p*s *> 0.10*

The first and last four trials in each condition were compared to determine if participants adequately learned the difference between the cues indicating reward vs. nonreward trials. A significant difference was noted in the 25s reward condition, $F$(1,163) = 5.117, $p$ = .025, with more accurate performance in the first four trials than in the last four trials. Here, performance in the last four trials was shifted such that mean reproductions were shorter than were the first four reproductions. Similarly, a significant difference was noted in the 25s nonreward condition, $F$(1,163) = 8.614, $p$ = .004, with more accurate performance in the first four trials than in the last

four trials. Here, performance in the last four trials was shifted such that mean reproductions were shorter than were the first four reproductions. Results were insignificant for the other four conditions.

Evaluation of exponents (see Table 5) indicates that hypothesis 1, that variation in timing of intervals is logarithmic and not linear in nature, was not supported. Two exponents (reward, nonreward conditions) were fit across all three time durations for each participant that completed trials in each time duration. In the reward condition, M = 1.01, SD = .24, nonreward M = 1.01, SD = .25. Neither best-fit exponent was significantly different from the null hypothesis of 1.00, $t(29) = .23$, $p = .82$ (reward), $t(29) = .18$, $p = .86$ (nonreward), nor were they significantly different from one another, $t(29) = .15$, $p = .88$.

Trial data was compared to predictions for both the best-fit linear and exponential functions across all three time durations, but separately for reward and nonreward. The actual reproduction minus the predicted reproduction was computed for all trials. With both the reward and nonreward conditions, the exponential functions predictions (reward M = .33, SD = 3.91, nonreward M = .30, SD = 3.88) significantly better fit the data than did the linear function predictions (reward M = -1.66, SD = 7.80, nonreward M = -6.03, SD = 4.87), $t(1798) = 12.18$, $p < .01$ (reward), $t(1786) = 85.74$, $p < .01$ (nonreward).

In total, these results indicate that hypothesis 1, that performance inaccuracy in reproduction of time intervals is logarithmic and not linear in nature as the duration of those intervals increases, was not supported. On the other hand, the observed increase in standard deviation with increasing time intervals was not linear. In total, further investigation is needed (see limitations of this study, below).

Hypothesis 3, that the value of the CV can change based on the presence or absence of reward, was not supported (all $p$s $> 0.10$). It was expected that the rewarded condition will lead

to smaller standard deviations in interval timing, indicating the effect of a shift in the value of the scalar operator. A nonsignificant trend in this direction was observed in all three time intervals.

Experiment 2 had several limitations. Though cash payouts to participants were more evenly distributed across the three time durations, several participants did ask the experimenters (after their participation was complete) if there was any meaning to the two different cues used in the experiment. Additionally, anecdotal evidence from participants indicates some found this hour-long task 'mind-numbingly boring', and thus may have reduced their attention to the task. Other anecdotal evidence suggests that the $0.10 payout per trial ($5.00 maximum) was neither enough to be rewarding in and of itself, nor enough to compensate for the 'punishment' of their hour-long participation in a task perceived as exceedingly boring. Thus, the intended reward in some cases may have instead acted merely to reduce perceived punishment.

## General Discussion

Findings from both experiments were largely in agreement with one another, indicating that mean reproductions were close to the actual time interval (regardless of the presence or absence of reward), that standard deviations increased as the time interval increased, but that there was no effect of reward on these means and standard deviations. Computational modeling (hypothesis 2) is discussed in Appendix D.

Both studies failed to indicate that timing variability is scalar in nature (Hypothesis 1), or that the CV changes based on the presence or absence of reward (Hypothesis 3). There was a nonsignificant trend in some durations in both Experiments 1 and 2 that mean reproductions were shorter in the reward condition than in the nonreward condition. This, again, may suggest that if timing is scalar in nature, the exponent has a value of less than 1, at least in rewarding situations – this is in agreement with the addage that 'time flies when you're having fun'.

Hypothesis 1, that performance inaccuracy in reproduction of time intervals is logarithmic and not linear in nature as the duration of those intervals increases, was not supported. Results supporting Hypothesis 1 would have provided supporting evidence for previous works suggesting an exponent value of approximately 0.9 in the nonreward condition (Allan, 1998; Malapani & Fairhurst, 2002). While the bulk of the literature suggests this is the case, a substantial minority suggest timing is linear, particularly in well-rehearsed participants (Allan, 1998; Bizo et al., 2006; Galtress et al., 2012). In the reward condition, we expected to observe a smaller value for the exponent, which would suggest that reward accelerates time perception (perhaps through pacemaker mechanisms like those involved in the pharmacologically altered time perception often observed after administration of dopamine agonists). Moreover, it was expected that the standard deviation of reproductions would be a constant fraction of the mean estimate in the nonreward condition. This would replicate the observation that interval timing follows Weber's Law (Allan, 1998). There are two possibilities in the reward condition. First, standard deviations of estimates could be a constant fraction of the mean. In this case, we expect reward to reduce the value of the fraction relative to the nonreward condition. Second, reward might produce standard deviations that are not a constant fraction of the mean. The failure to support Hypothesis 1 in the present study could lend credence to those suggestions, and would be indicative of the need for further research in this area. This failure to support Hypothesis 1 could be attributable to either interval timing truly not having scalar components, or to a failure of the filler task in this experiment to adequately distract participants – if participants were able to accurately 'count off' time during the experiments, results may be skewed towards showing linear trends. Nonetheless, the findings that predictions from best-fit

exponential functions better fit the data than did predictions from best-fit linear functions (except in Experiment 1 nonreward) are promising, and warrant further investigation.

Failure to support Hypothesis 3 is potentially problematic for theories of interval timing that suggest a neural overlap and interplay of these processes with those of reward processing (e.g. Galtress et al., 2012). This failure to support Hypothesis 3 could be indicative of either no interplay between these systems or processes or a failure to adequately motivate participants in the experimental group. Further investigation, correcting the limitations of the present study, is necessary to fully investigate this question. Here, increasing the value of the reward from $.10 per trial to some significantly higher value may be of benefit.

Further, the present study investigates interval timing using visual cues. As Lustig and Meck (2011) indicate that the performance of adult humans varies when presented with cues in different sensory modalities, future research should compare results using a variety of sensory modalities for cues while holding all other experimental conditions and settings constant. A further limitation of the present study is the use of second-scale timing intervals. Others have reported that different timing processes operate in millisecond time scales relative to second time scales (Bangert et al., 2011). The literature is also silent on the estimation of hours-long time scales. Future studies should investigate both of these time scales, both experimentally and neurocomputationally, with the goal of elucidating what timing mechanisms operate on these scales. Additionally, as Bangert et al. (2011) found evidence of linear variation in timing for intervals up to one second, and a shift to scalar variation thereafter, future research should investigate the mechanisms of this shift between timing mechanisms. Finally, as the neurotransmitter acetylcholine (ACh) is known to influence both timing (Hinton & Meck, 1997)

and long-term memory (Grossberg & Schmajuk, 1989), future work should incorporate mathematical representations of ACh activity as related to interval timing.

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# Appendix A

## Opt-out and experimental rationale provided to each participant

The following text was presented on the computer screen as each participant began the experiment. For Experiment 2, text involving random number generation was replaced with text about the serial math task:

"Thank you participating in this experiment. You will receive instructions for performing your tasks on the screen, followed by a brief training session, followed by the experimental tasks.

You will be asked to generate a series of random numbers during a variety of randomly generated time periods. The total time to complete this experiment is approximately 45 to 60 minutes. The PC will indicate the time interval to be estimated by presenting visual cues, followed by a timed pause, followed by more visual cues. Next, you will be asked to tap the spacebar on the computer keyboard, marking the beginning of your estimation of that time period.

Next, you will then write as many random numbers as possible, using the pen and paper provided, in the amount of time you estimate that equals the reference time duration. You will then again tap the computer keyboard spacebar to indicate the end of this time period. As we are investigating the effects of cognitive load on random number generation in various time periods, it is important that you estimate the time interval accurately. Please do your best to ensure the numbers you provide on paper are random and not sequential or otherwise structured.

Your participation is voluntary, and you have the right to quit this experiment at any time, should you choose to do so. All responses and data collected are confidential, and are not traceable back to you.

Thank you again for your participation, and feel free to direct any questions or concerns to the experimenter before continuing."

“On the table in front of you is a pen and a stack of blank paper. Please write your participant number at the top left of the top page.

During each trial, you will be presented with a visual cue. Next, you will be asked to press the spacebar on the PC, then generate a series of random numbers on the paper provided. Please use numbers of at least two digits, with no number consisting of the same number of digits as the previous number.

While writing these numbers, keep track of the reference time interval as best as you can. At the end of this period, press the computer keyboard spacebar to indicate the end of the time period. Again, please try to be as accurate as possible. You will earn a token quantity of cash money as a reward for your accuracy (up to $5.00).

After completing each trial, please draw a line under the last random number you generated so as to keep the groups of numbers separate.”

# Appendix B

## Math Task – Representative Page of Math Problems

Participant ID #:_____

**Please complete as many problems as possible while estimating each time interval duration**

Use one block of math problems per trial. Move to a new block for each trial.

| | | | | |
|---|---|---|---|---|
| 4 - 6 | 6 x 8 | 9 x 3 | 6 + 2 | 5 - 6 |
| 7 + 4 | 7 - 6 | 4 - 6 | 7 - 6 | 9 + 7 |
| 7 + 4 | 3 - 5 | 4 x 7 | 6 - 2 | 7 + 2 |
| 3 + 4 | 5 x 6 | 4 - 9 | 9 + 8 | 5 + 2 |
| 8 - 6 | 3 x 7 | 8 x 7 | 5 - 7 | 6 - 2 |
| 8 + 7 | 4 - 7 | 2 + 9 | 4 - 3 | 8 + 4 |
| 8 + 6 | 5 - 2 | 4 + 3 | 2 - 5 | 7 + 2 |

| | | | | |
|---|---|---|---|---|
| 8 - 3 | 3 + 2 | 8 x 9 | 6 - 6 | 3 - 8 |
| 5 + 2 | 3 + 8 | 4 x 3 | 5 x 8 | 4 + 2 |
| 4 + 7 | 8 + 9 | 3 - 8 | 9 + 8 | 2 + 5 |
| 8 x 7 | 4 x 2 | 5 + 4 | 2 - 7 | 5 x 2 |
| 9 - 7 | 5 + 4 | 9 x 4 | 5 - 6 | 3 - 9 |
| 7 + 3 | 7 - 6 | 3 - 2 | 8 - 8 | 9 + 3 |
| 8 + 4 | 3 + 7 | 2 x 7 | 5 - 2 | 2 + 4 |

| | | | | |
|---|---|---|---|---|
| 6 x 7 | 5 x 4 | 5 x 9 | 5 x 6 | 6 x 9 |
| 9 + 2 | 7 + 4 | 3 + 5 | 3 - 9 | 4 + 4 |
| 4 - 5 | 7 x 4 | 7 x 6 | 5 + 8 | 6 - 5 |
| 4 - 6 | 4 - 4 | 7 - 9 | 9 + 3 | 9 - 5 |
| 3 - 8 | 5 - 6 | 9 + 6 | 3 + 5 | 9 - 6 |
| 5 + 6 | 2 x 2 | 3 + 6 | 2 x 3 | 6 + 2 |
| 7 + 5 | 5 x 4 | 2 x 8 | 5 - 6 | 6 + 7 |

| | | | | |
|---|---|---|---|---|
| 7 x 4 | 6 + 9 | 5 + 2 | 4 - 2 | 2 x 5 |
| 8 x 5 | 2 + 7 | 6 x 5 | 6 - 4 | 3 x 9 |
| 8 - 9 | 7 + 3 | 9 + 4 | 2 - 9 | 4 - 2 |
| 2 - 6 | 5 - 9 | 9 - 9 | 7 + 6 | 9 - 9 |
| 5 x 6 | 2 - 2 | 6 - 6 | 7 x 4 | 8 x 4 |
| 4 x 6 | 7 - 6 | 5 x 8 | 5 + 4 | 9 x 7 |
| 8 + 4 | 7 + 8 | 2 x 2 | 6 - 5 | 3 + 8 |

| | | | | |
|---|---|---|---|---|
| 9 + 6 | 3 - 6 | 3 - 4 | 8 - 7 | 7 + 7 |
| 4 - 3 | 2 - 3 | 8 + 7 | 2 + 9 | 9 - 8 |
| 3 x 3 | 4 - 2 | 5 + 3 | 2 + 7 | 8 x 5 |
| 7 - 8 | 5 - 5 | 8 - 6 | 8 - 6 | 8 - 2 |
| 8 + 4 | 2 - 7 | 3 + 2 | 3 - 5 | 7 + 4 |
| 8 - 9 | 9 + 8 | 7 - 3 | 7 - 3 | 4 - 3 |
| 2 x 9 | 6 - 3 | 6 x 9 | 6 + 4 | 9 x 8 |

| | | | | |
|---|---|---|---|---|
| 8 - 4 | 5 - 9 | 9 + 9 | 2 - 8 | 9 - 2 |
| 2 + 4 | 4 x 5 | 3 x 4 | 5 + 3 | 6 + 8 |
| 7 - 4 | 8 + 2 | 7 x 7 | 6 - 6 | 4 - 9 |
| 3 - 4 | 5 - 9 | 7 + 4 | 2 + 4 | 8 - 2 |
| 3 - 5 | 6 x 4 | 8 - 6 | 8 + 7 | 6 - 6 |
| 8 x 8 | 7 - 2 | 5 - 7 | 7 - 7 | 8 x 6 |
| 3 - 5 | 8 x 5 | 8 + 4 | 3 + 4 | 5 - 5 |

Each participant in Experiment 2 was provided with 20 pages of math problems as a filler task during time interval reproduction trials. Each page contained six blocks of 35 math problems each. Math problems consisted of addition, subtraction, and multiplication of single-digit integers. For each trial, participants were instructed to complete as many problems as possible during their reproduction of the the reference time interval. Participants were asked to move to the next block on each new trial. The primary investigator watched participants complete this task over the course of the experiment to ensure compliance.

# Appendix C

## All Participants

Experiments 1 and 2 used the first 19 and last 41 of 133 total participants, with participants 20 – 91 participating in pilot studies while developing the parameters used in Experiment 2. Changes between Experiments 1 and 2 involved a change in the filler task (moving from random number generation to serial math problems) and changes in how many trials in each condition the PsychoPy program presented to participants. In post-hoc analyses, data from all 133 participants was evaluated using the type of filler task as a factor (random number generation, n = 61, serial math task, n = 72). In no case was there a significant result based in the type of filler task used. These analyses were conducted using the same elimination criteria as detailed in Experiments 1 and 2.

Participants' performance was evaluated in a 2 (Filler task [random numbers vs. math problems]) x 2 (Reward [reward vs. nonreward]) x 3 (Interval [5, 15, 25 s]) ANOVA. Analyses indicated an effect of duration (5, 15, 25 s), $F$ (2, 147) = 3077.1, $p < .01$ (see Figure 12), but neither an effect reward, $F$(1, 148) = 1.73, $p$ = .19, nor interaction between duration and filler task, $F$(2,147) = 0.41, $p$ = .67, effect of effect interaction of reward and filler task, $F$(1, 148) = 0.09, p = .77, effect of interaction between reward and duration, $F$ (2, 147) = 0.57, $p$ = .57, nor effect of interaction between duration, reward, and filler task, $F$(2, 147) = 0.63, $p$ = .54.

Means, standard deviations, and CVs are shown in Table 4. Though neither predicted nor significant, it is interesting to note that in 5 and 15 (but not 25 s) durations the mean reproductions were shorter in the reward condition than in the nonreward condition (Figure 13). No significant difference in CVs between the reward and nonreward conditions within each interval were found: $F$(1, 105) = 2.12, $p$ =.15 (5 s); $F$(1, 99) = .11, $p$ = .74 (15 s); $F$(1, 95) = 1.36, $p$ = .25 (25 s). Additionally, as CVs are a function of mean and SD, means and SDs were

correlated in both the reward and nonreward conditions, $r(301) = .67$, $p < .01$ (reward), $r(301) = .70$, $p < .01$ (nonreward), and a best-fit linear function was derived through linear regression across all three time intervals, but separately for reward and nonreward. See Figure 14.

The first and last four trials in each condition were compared to determine if participants adequately learned the difference between the cues indicating reward vs. nonreward trials. Results were nonsignificant in all cases.

Evaluation of exponents (see Table 5) indicates that hypothesis 1, that performance inaccuracy in reproduction of time intervals is logarithmic and not linear in nature as the duration of those intervals increases, was not supported. Two exponents (reward, nonreward conditions) were fit across all three time durations for each participant that completed trials in each time duration. In the reward condition, M = 1.02, SD = .23, nonreward M = 1.02, SD = .26. Neither best-fit exponent was significantly different from the null hypothesis of 1.00, $t(78) = .87$, $p = .39$ (reward), $t(78) = .75$, $p = .46$ (nonreward), nor were they significantly different from one another, $t(78) = .11$, $p = .92$.

Trial data was compared to predictions for both the best-fit linear and exponential functions across all three time durations, but separately for reward and nonreward. The actual reproduction minus the predicted reproduction was computed for all trials. With both the reward and nonreward conditions, the exponential function predictions (reward M = -0.19, SD = 4.31, nonreward M = -0.19, SD = 4.32) significantly better fit the data than did the linear predictions (reward M = -4.54, SD = 4.65, nonreward M = -4.50, SD = 4.59), $t(4323) = 138.18$, $p < .01$ (reward), $t(4316) = 144.19$, $p < .01$ (nonreward).

Hypothesis (#3), that the value of the CV can change based on the presence or absence of reward, was not supported. It was expected that the rewarded condition will lead to smaller standard

deviations in interval timing, indicating the effect of a shift in the value of the scalar operator. A nonsignificant trend in this direction was observed in the 5s and 15s time intervals. On the other hand, the observed increase in standard deviation with increasing time intervals was not linear. In total, further investigation is needed (see limitations of this study in the general discussion).

# Appendix D

## Computational Modeling

Though our model is named Real Time Comparator Model (RTCM), computers perform mathematical operations in discrete steps, they cannot truly simulate 'real time'. Instead, the RTCM model divides the trial into many smaller discrete events, which are computationally represented in array form. These discrete events are modeled spectrally such that they conceptually reflect a CS activating a population of neurons, with members of that population firing at different rates (e.g. Grossberg & Schmajuk, 1989; Hopson, 1999). Spectral timing models have been used to describe neuron population activity in cerebellar Purkinje cells (Fiala, Grossberg, & Bullock, 1996) and in cortico-basal ganglia timing circuits (Jin, Fujii, & Graybiel, 2009), suggesting conceptual validity for their inclusion in the present RTCM model.

The purpose of the present simulations was to test whether this real-time extension of SOCR can explain timed behavior and the distribution of variation across an interval. Table 1 summarizes the SOCR equation system.

In a study of conditioned responses, Drew et al. (2005) trained two groups of goldfish, *Carassius auratus*, ($n$ = 18 per group) through exposure to light-shock pairings with 5 s ('short' group) or 15 s ('long' group) inter-stimulus intervals (ISIs). Sessions (n = 20) consisted of reinforced, blank, and peak trials in random order (though with no more than two reinforced or blank trials occurring successively). In reinforced trials, the light (CS) was followed either 5 or 15 s later (ISI) by an electrical shock (US), neither CS nor US were presented in blank (baseline) trials. Peak trials involved CS presentation for 45 s without any following US. Behavioral response was a measured as a function of intensity and frequency of the fishes' responses. Drew

et al. (2005) report that responses increased as a function of session and differed as a function of ISI (see Figure 15).

In an initial test utilizing the RTCM model, Drew et al.'s (2005) data were programmed into MATLAB. There, the RTCM model provided a best fit to the data based upon Drew et al.'s (2005) trial structure and optimization of free parameters in the SOCR model. Based on the fit of RTCM predictions to the observed data, this model appears to explain the timed conditioned responses (see Figure 15). The present study aimed to further test the fit of the RTCM model to observed data. Thus, the RTCM model is proposed as a means to describe the nature and means of interval timing and interval timing variability.

Though relatively new, previous iterations of the SOCR model have accurately predicted performance, relative to competing models, in various learning paradigms (Stout & Miller, 2007; Witnauer et al. 2014) and in initial testing based on Drew et al.'s (2005) data as discussed above. Failure to find support for Hypothesis 2(concerning the scalar nature of timing) in this experiment may suggest that other models, such as TD (Schultz, 2013), may be more accurate in predicting performance in timing tasks.

Hypothesis 2 was evaluated in MATLAB. First, the RTCM model was loaded into MATLAB. This model allowed the scalar value to vary, and the model's output provided a scalar value and the sum of squared error (SSE) for all participants in all trials, separately for both experiments. The SOCR model (Stout & Miller, 2007; Witnauer et al., 2014) considers a lack of cue competition in trials, positive and negative mediation, and comparator processes not incorporated in the TD model. As some of these processes (e.g., the comparator) are largely incorporated in scalar timing models (Arantes, 2008; Machado & Arantes, 2006), it was expected that RTCM would provide a scalar value close that reported in the literature (approximately 0.9).

The RTCM model predictions were as expected, with predictions for the scalar (exponent) ranging between 0.87 and 0.92 (see Table 5). Additionally, exponents were smaller in the reward than the nonreward condition, again suggesting a faster perception of time passage in rewarding (or 'fun') circumstances. However, observed exponents from Experiments 1, 2, and from all participants in aggregate were higher than predicted (range: 1.01 to 1.15). This difference may be rooted in the high variability observed in the collected data, and may be more a function of low pereceived reward value in the reward condition rather than a true scalar value of $\approx 1.00$ as indicated by the data.

Additionally, as a function of this scalar, the RTCM model predicted that for each time duration, peak responses occurred earlier in the reward condition than in the nonreward condition (see Figure 16). This difference in response times was not observed in all time durations in all Experiments, though these observed differences were not significant.

Additional work is neceassry to confirm the model's accuracy. The fact that the observed exponent value in all Experiments exceeded 1.00 in all cases may suggest that participants found the timing task punishing (or at least nonrewarding) in both conditions. Further work should aim to improve the perceived reward in the reward condition. After development of a task truly perceived as rewarding (in the reward condition), further comparisons to model predictions should be evaluated.

As work continues in developing a SOCR model with stronger biological constraints (Witnauer et al., 2014), finding support for Hypothesis 2 in this study would suggest further use of computational modeling as a means for inferring how neural systems operate, and in fully associating cognitive processes with their neural bases. As a model can indicate what processes a

neural system likely performs in a task, we can better match these cognitive processes with what is known about the operation of specific brain regions and systems

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Table 1

*Model Equations*

| Model | Equation |
|---|---|
| Rescorla-Wagner | $\Delta V_{x,o} = \alpha_x * \beta_o(\lambda_o - \sum V_i)$<br>$\beta_o = \beta_{up}\ when\ \lambda_o > 0$<br>$\beta_o = \beta_{down}\ when\ \lambda_o = 0$<br>$R_x \approx V_{x,o}$ |
| SOCR | $\Delta V_{s1,s2} = s1 * s2 * (1.0 - V_{s1,s2})\ when\ s1 > 0\ and\ s2 > 0$<br>$\Delta V_{s1,s2} = -k * s1 * V_{s1,s2}\ when\ s1 > 0\ and\ s2 = 0$<br>$Op_{x,j,o} = 1.0 - Op_{x,j,o}\ when\ V_{x,o} > 0$<br>$Op_{x,j,o} = \alpha_x * k3 * V_{x,j} * V_{j,o} * (1.0 - Op_{x,j,o})\ when\ V_{x,o} = 0$<br>$R_x = V_{x,o} - k2 * [\sum Op_{x,j,o} * r(V_{x,j}) * r(V_{j,o})]$ |
| RTCM | $Response_j = V_{i-outcome} - k\,(Op_{i,j,outcome} \times V_{i,j} \times V_{j,outcome})$<br>$\Delta V_{i,j} = Activation_i \times Activation_j\ \ when\ s1 > 0\ and\ s2 > 0$<br>$\Delta V_{i,j} = Activation_i \times Activation_j \times k\ \ when\ s1 > 0\ and\ s2 = 0$ |

*Note.* $V$ = associative strength; $\alpha_x$ and $\beta_o$ are learning-rate parameters; $\lambda_o$ is the maximum associative strength supportable by a given outcome on a single trial; $R$ = response; *s1* and *s2* are saliences of *S1* and *S2*; *k1* is a decremental learning-rate parameter applied on trials on which the outcome *S2* is absent; *j* = all cues except *X* and *O*; $Op_{x,j,o}$ = the switching operator. Rescorla-Wagner and SOCR equations are adapted from Stout and Miller (2007, p.764)

Table 2

*Experiment 1 - Means, standard deviations, and coefficients of variation*

| **Condition** | **Mean** | **SD** | **CV** |
|---|---|---|---|
| 5s Reward | 4.752 | 1.530 | 0.322 |
| 5s Nonreward | 4.908 | 1.653 | 0.337 |
| 15s Reward | 14.541 | 3.900 | 0.268 |
| 15s Nonreward | 13.733 | 4.838 | 0.352 |
| 25s Reward | 25.831 | 6.064 | 0.235 |
| 25s Nonreward | 26.206 | 6.590 | 0.251 |

Table 3

*Experiment 2 - Means, standard deviations, and coefficients of variation*

| **Condition** | **Mean** | **SD** | **CV** |
|---|---|---|---|
| 5s Reward | 5.600 | 1.622 | 0.290 |
| 5s Nonreward | 5.657 | 1.613 | 0.285 |
| 15s Reward | 15.763 | 3.296 | 0.209 |
| 15s Nonreward | 15.727 | 3.436 | 0.218 |
| 25s Reward | 25.952 | 5.520 | 0.213 |
| 25s Nonreward | 25.872 | 5.406 | 0.209 |

Table 4

*All participants - Means, standard deviations, and coefficients of variation*

| **Condition** | **Mean** | **SD** | **CV** |
|---|---|---|---|
| 5s Reward | 5.438 | 1.390 | 0.256 |
| 5s Nonreward | 5.510 | 1.451 | 0.263 |
| 15s Reward | 15.664 | 3.249 | 0.207 |
| 15s Nonreward | 15.672 | 3.298 | 0.210 |
| 25s Reward | 26.047 | 6.424 | 0.247 |
| 25s Nonreward | 25.977 | 6.382 | 0.246 |

Data from all participants.

Table 5

*Exponents*

| | **Model Predictions** | **Experiment 1** | **Experiment 2** | **All Participants** |
|---|---|---|---|---|
| **Condition** | **Exponent** | **Exponent** | **Exponent** | **Exponent** |
| All durations Reward | 0.87 | 1.04 | 1.01 | 1.02 |
| All durations Nonreward | 0.92 | 1.15 | 1.01 | 1.02 |

Predicted exponents and peak response times from the RTCM model and observed exponents and peak response times from Experiments 1, 2, and from all 133 participants. The last two rows present the best-fit exponent across all three time durations.

Figure 1

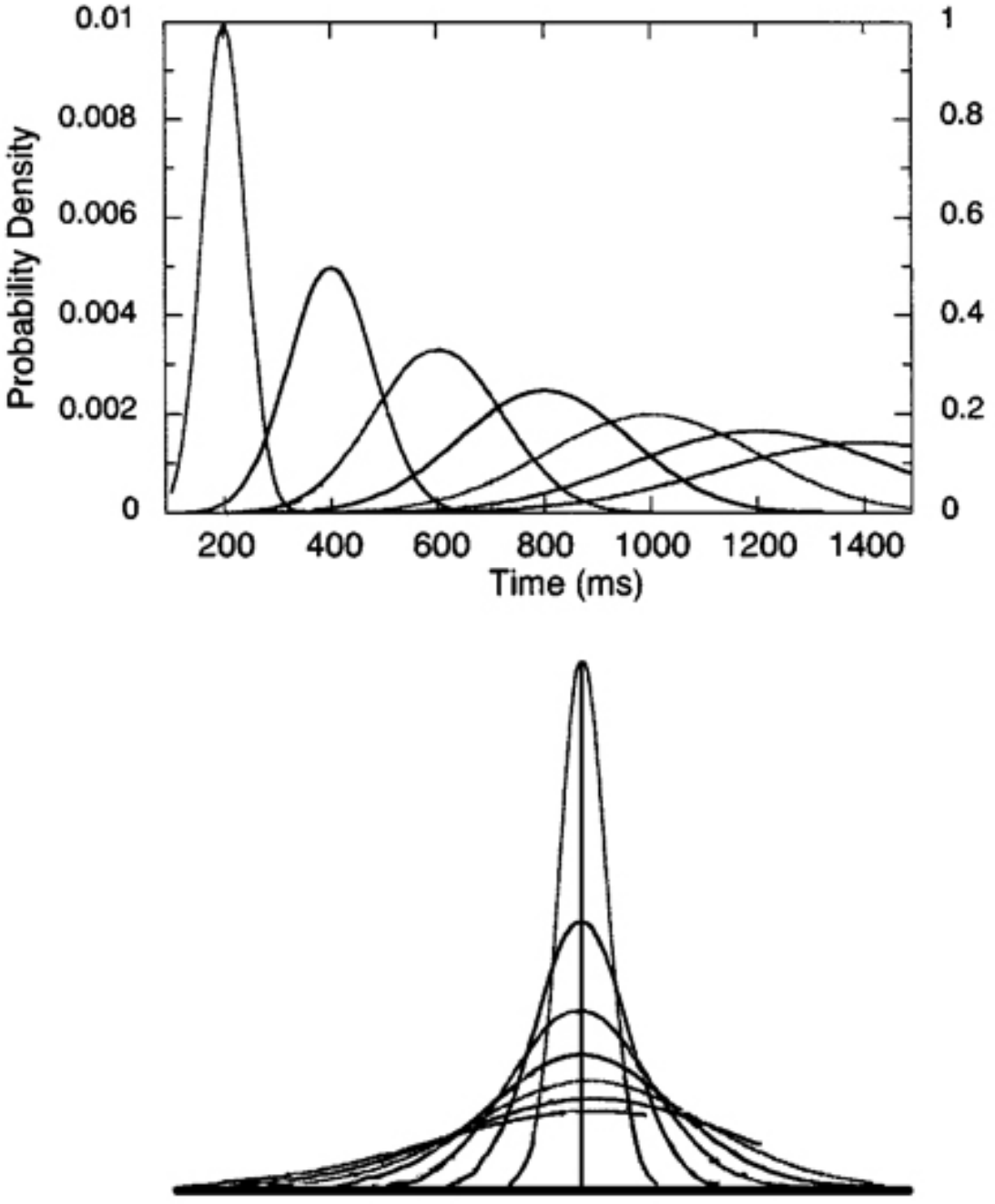


*Figure 1*: Top: In a time interval estimation or reproduction task, the standard deviation (σ) increases as a function of the mean. Bottom: Superimposition of the curves. Adapted from Killeen (2002, p.64).

Figure 2

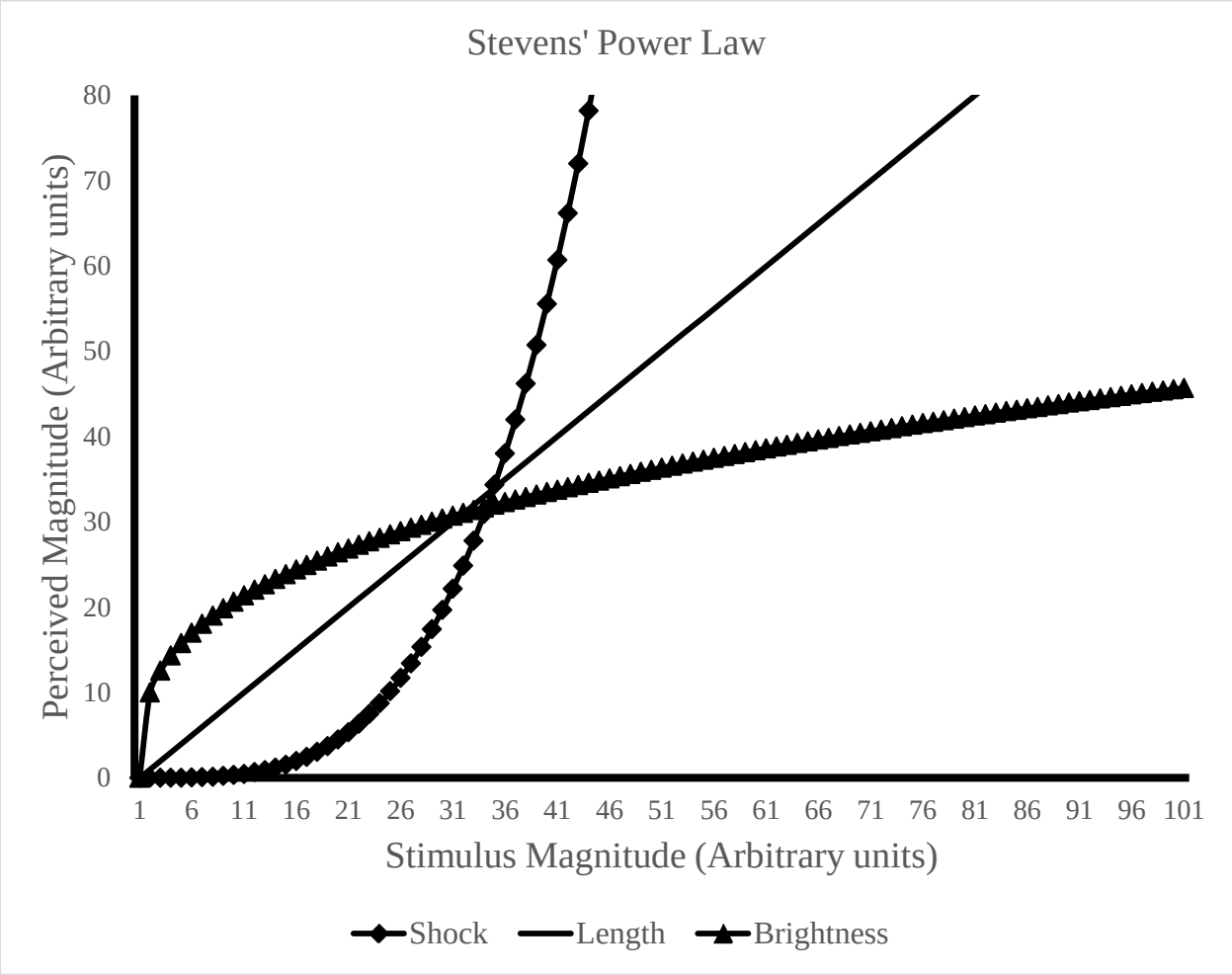


*Figure 2:* Stevens' psychophysical law, also called the power law, mathematically describes how perception of a stimulus changes as function of change in the intensity of that stimulus. In the generalized form,

$$Perceived\ magnitude = K * Stimulus\ magnitude^{Exponent}$$

where *K* is constant (specific to a given sensory modality) and *Exponent* changes for each stimulus perception type. In example, Stevens (1957, 1960) indicates that *Exponents* for perception of electrical shock intensity, visual perception of line length, and visual perception of brightness are 3.5, 1.0, and 0.33, respectively. The values of *K* for these stimuli are .00015, 1, and 10, respectively. Graph adapted from Stevens (1960, p. 237).

Error, or variance, in perceived magnitude of a stimulus is described by Weber's law, in the generalized form:

$$Coefficient\ of\ variation = \frac{\Delta I}{I}$$

where *I* is the magnitude of a stimulus, and *ΔI* is the amount of change in stimulus intensity needed to affect a just-noticeable perceived change in intensity of that stimulus. In example, an individual holding a 100 g weight will generally not perceive a change in that weight if a 1 g weight is added, but will generally notice a difference in perceived weight when a 2 g weight is added to the 100 g weight. Thus, *ΔI* = 2 and *I* = 100, resulting in a coefficient of variation of .02.

As applied to error in time duration perception,

$$\text{Coefficient of Variation} = \frac{\sigma}{t}$$

where σ is the standard deviation of time interval estimates or reproductions and *t* is the mean of those time interval estimates (Bizo et al., 2006; Gibbon, 1977).

Figure 3

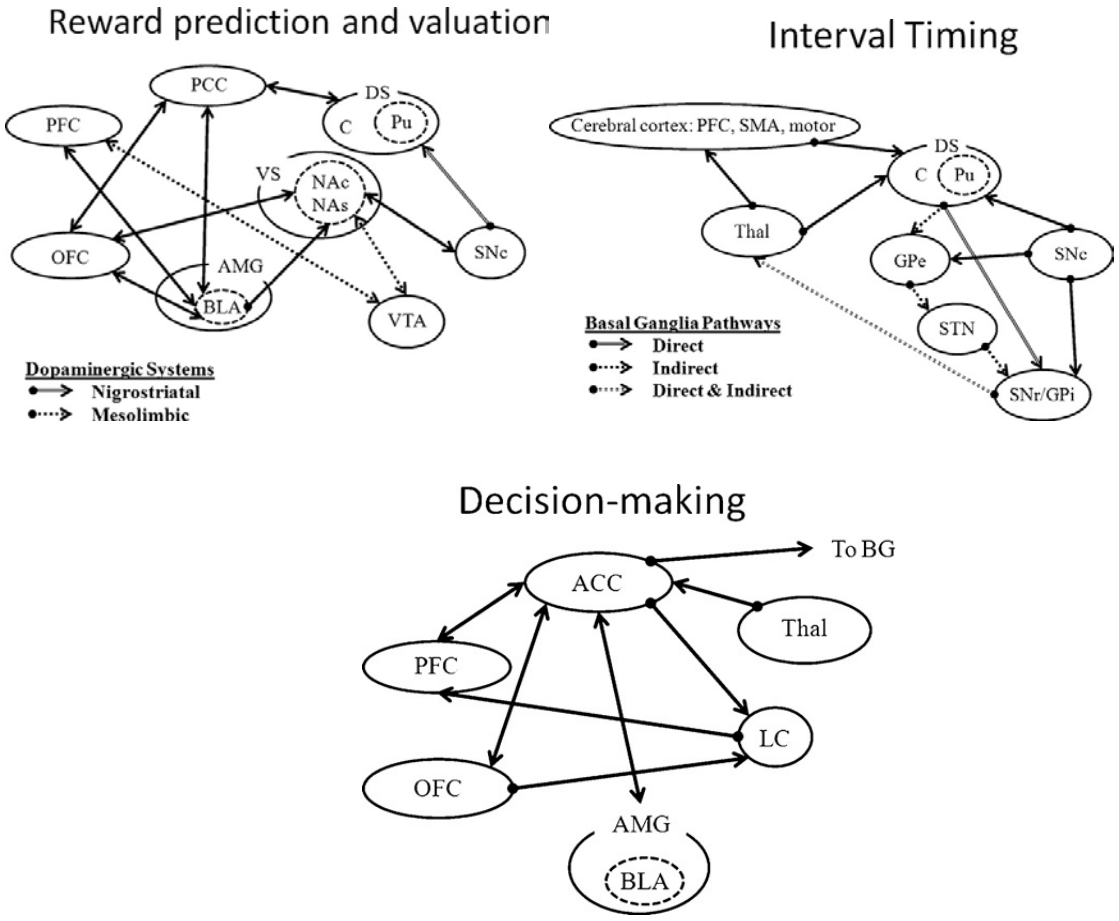


*Figure 3*: Overlap between the interval timing, reward prediction, and decision making neural substrates (Galtress et al., 2012, pp. 148-149). Abbreviations: Prefrontal Cortex (PFC), Orbitofrontal Cortex (OFC), Posterior Cingulate Cortex (PCC), Dorsal Striatum (DS), Caudate (C), Putamen (Pu), Ventral Striatum (VS), Nucleus Accumbens shell (NAs), Nucleus Accumbens core (NAc), Substantia Nigra pars compacta (SNc), Ventral Tegmental Area (VTA), Amygdala (AMG), Basolateral nucleus of the amygdala (BLA), Supplementary Motor Area (SMA), Thalamus (Thal), Subthalamic Nucleus (STN), Globus Pallidus internal (GPi), Globus pallidus external (GPe), Substantia Nigra par reticulata (SNr), Anterior Cingulate Cortex (ACC), and Locus Coeruleus (LC).

Figure 4

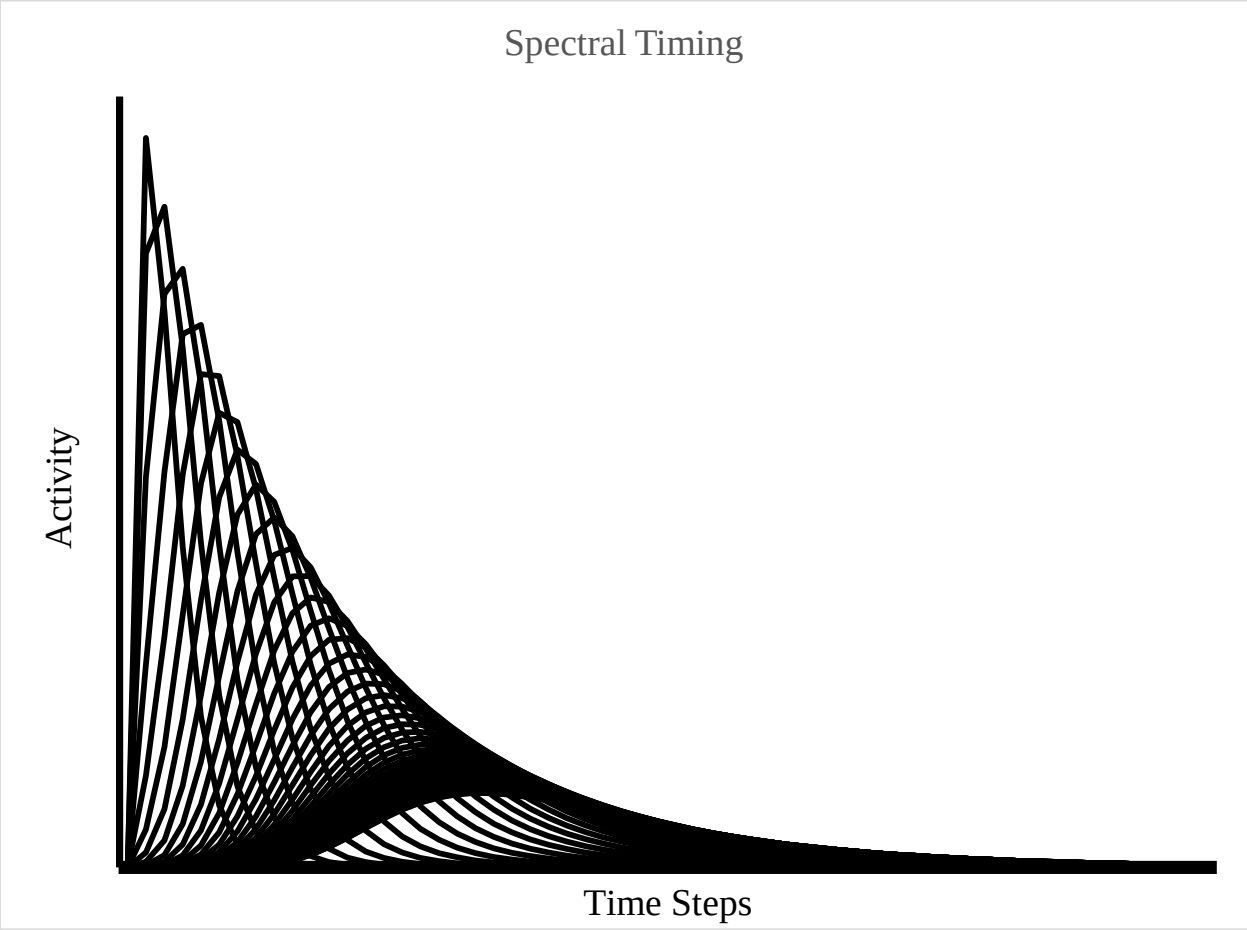


*Figure 4*: Spectral timing as performed by RTCM with 50 microelements responding to a stimulus.

Figure 5

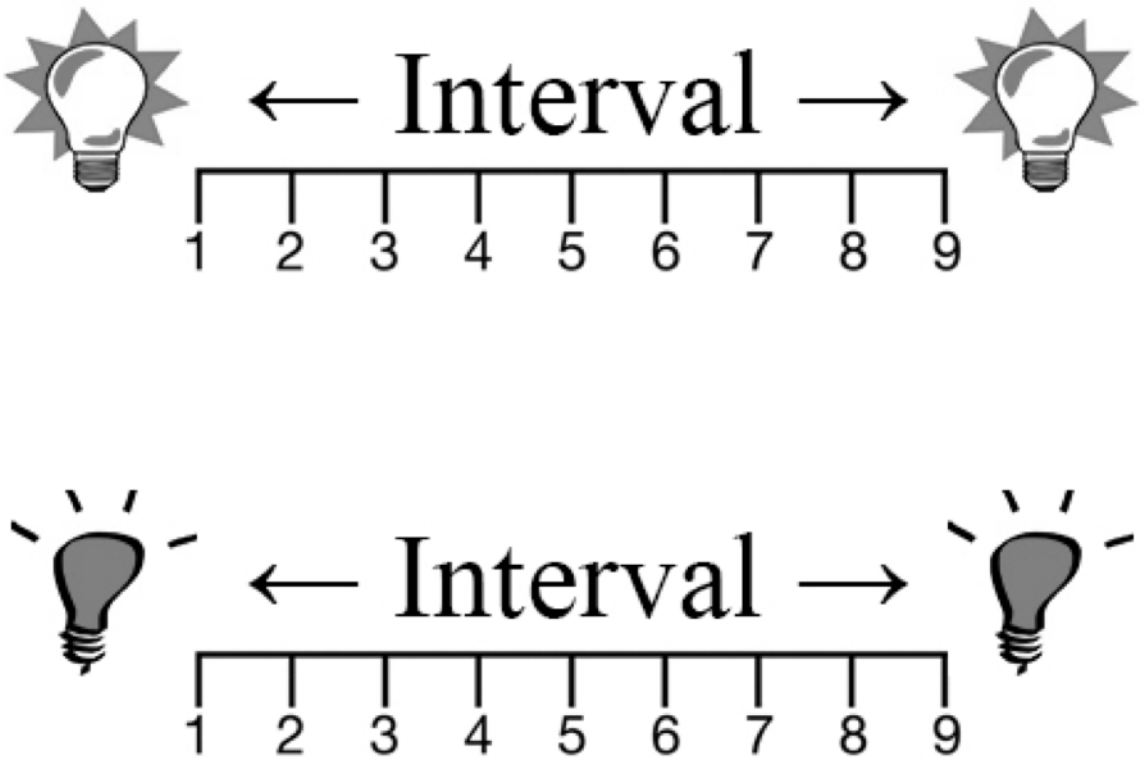


*Figure 5*. Top: Nonrewarded trials began with the presentation of a visual cue, followed by a timer counting off the reference time interval that the participant were asked to reproduce, then another presentation of the visual cue, signaling the end of the reference time interval. Bottom: Rewarded trials are identical to nonrewarded trials, except that an alternate visual cue was presented.

Figure 6

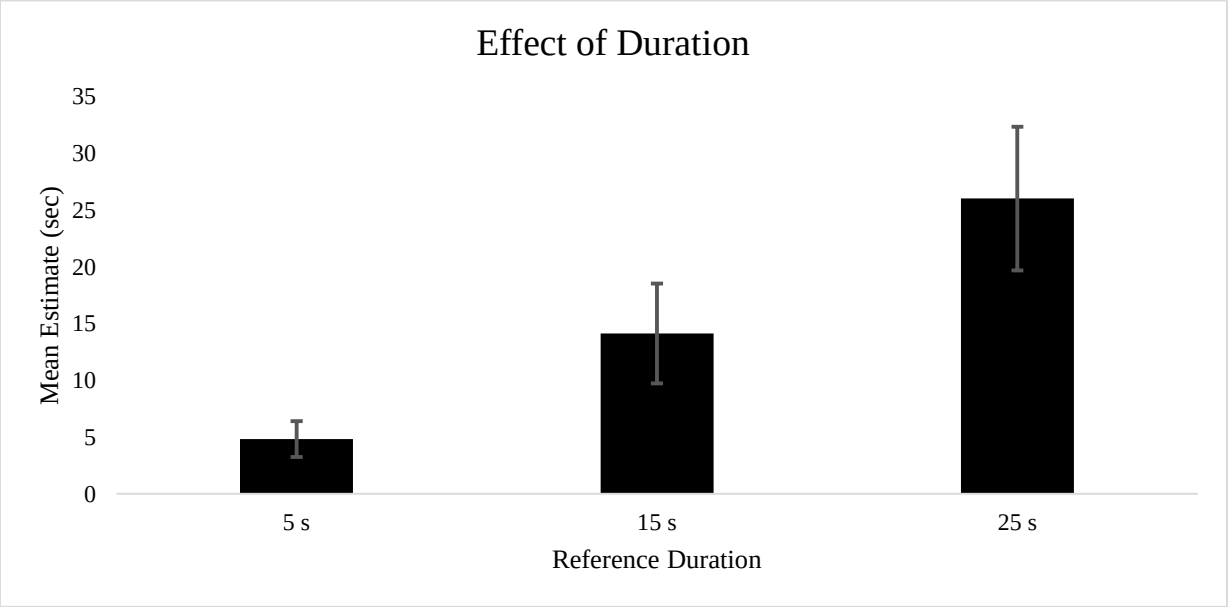


*Figure 6*. Main effect of duration in Experiment 1: For all trials at 5 s in duration, M = 4.83 s, SD = 1.42 s; for all 15 s trials, M = 15.67 s, SD = 3.27 s; for all 25 s trials, M = 26.01 s , SD = 6.40 s. Error bars are 1 SD.

Figure 7

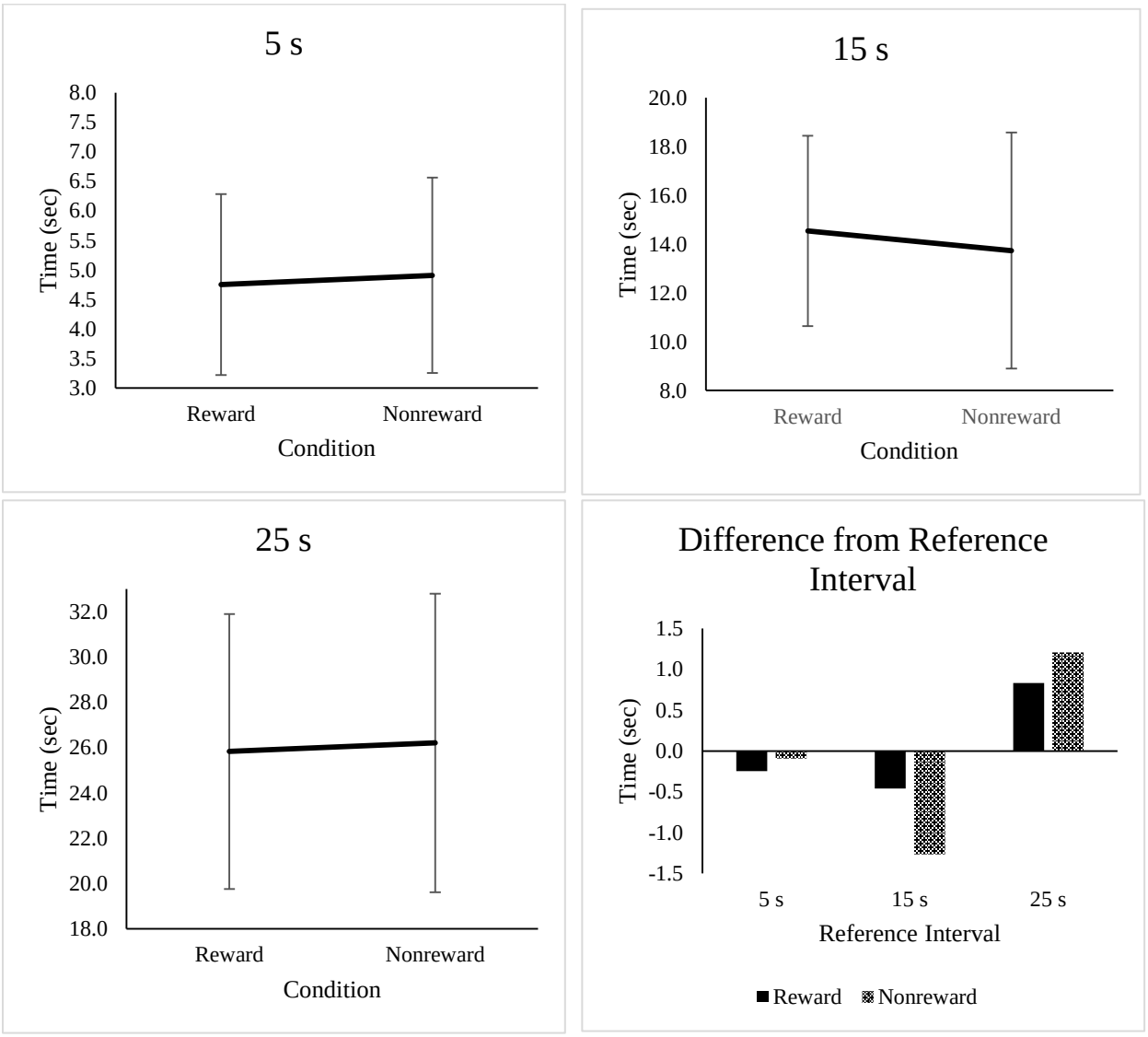


*Figure 7*. Experiment 1: Though insignificant, time estimates in the reward condition were shorter than in the nonreward condition. Error bars are 1 SD.

Figure 8

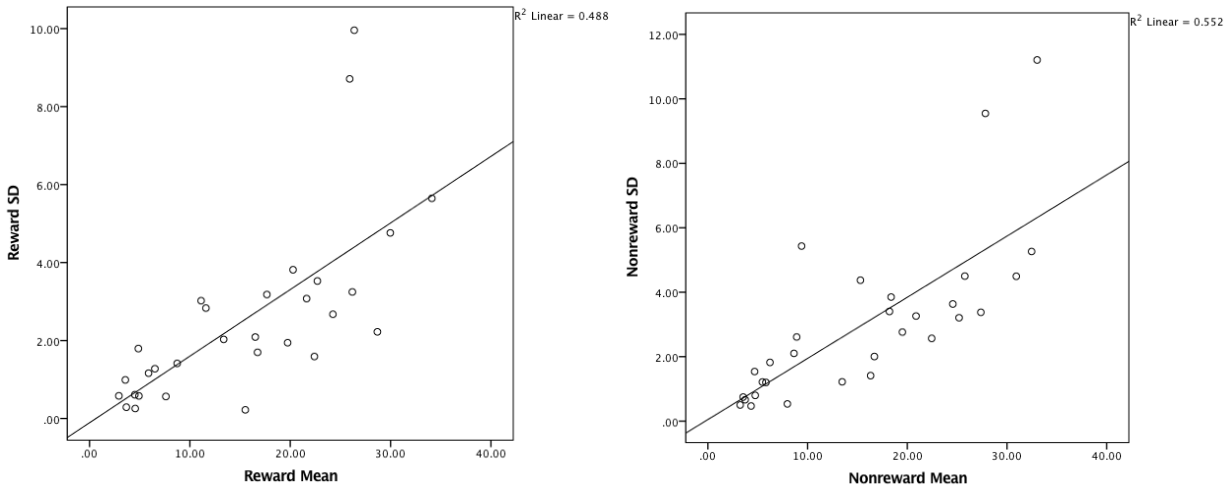


*Figure 8*: Experiment 1. Left: Correlation of means and SDs in the reward condition for all three time durations. The best linear fit is y = -0.11 + 0.17 * x. Right: Correlation of means and SDs in the nonreward condition for all three time durations. The best linear fit is y = 0.05 + 0.19 * x.

Figure 9

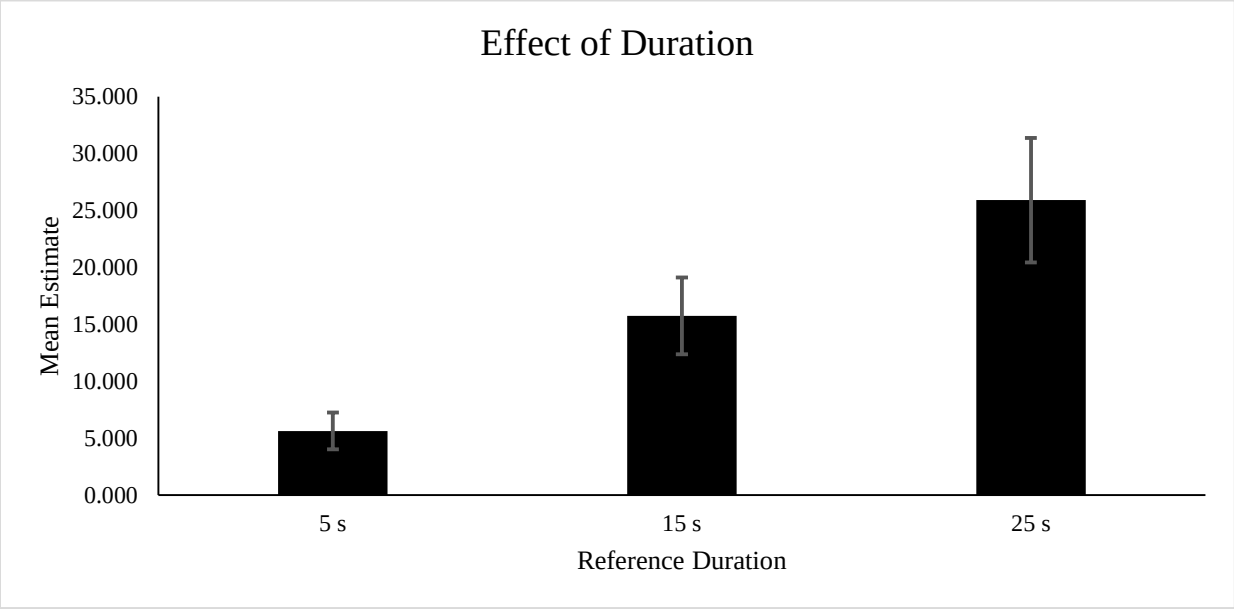


*Figure 9*. Main effect of duration in Experiment 2: For all trials at 5 s in duration, M = 5.63 s, SD = 1.62 s; for all 15 s trials, M = 15.75 s, SD = 3.67 s; for all 25 s trials, M = 25.91 s, SD = 5.46 s. Error bars are 1 SD.

Figure 10

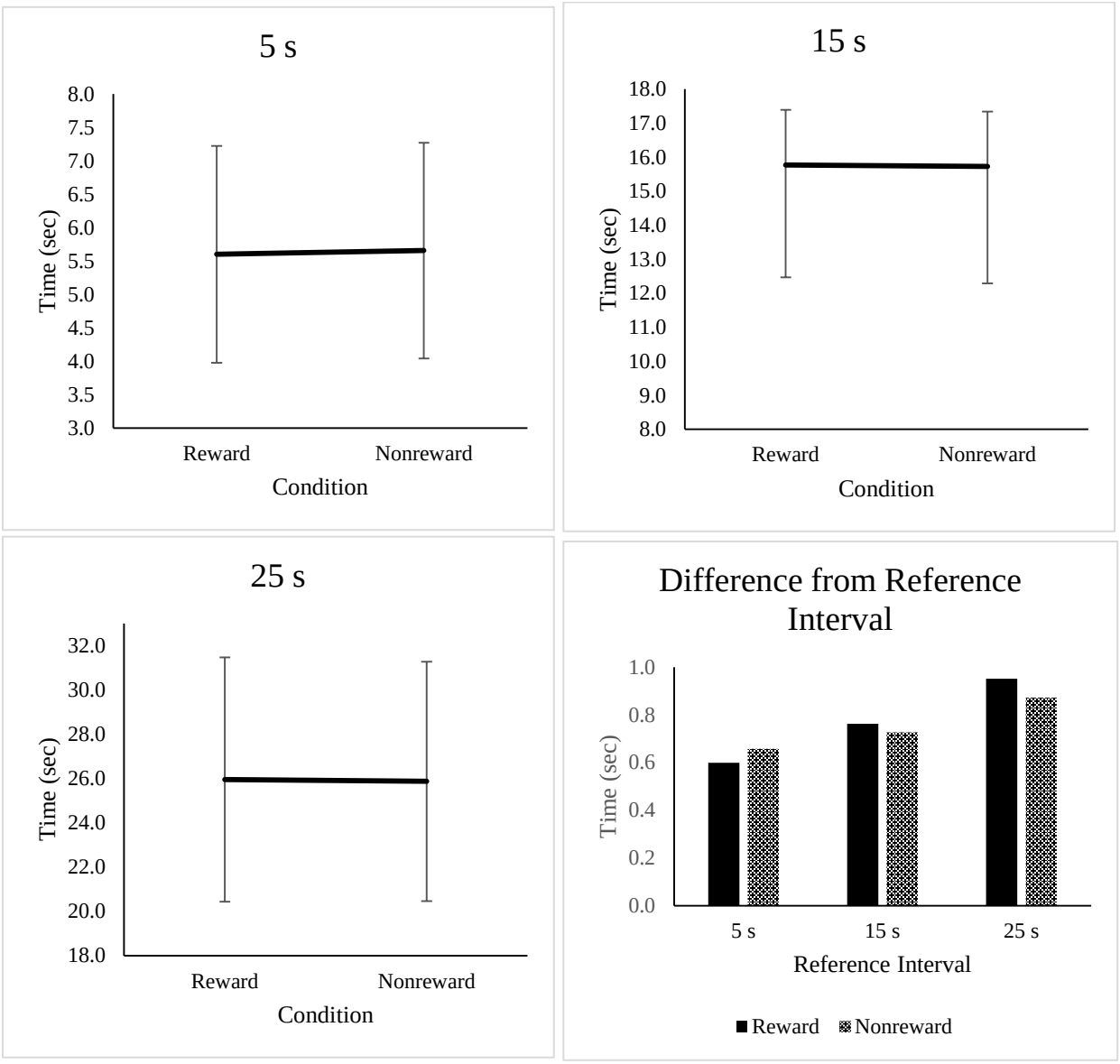


*Figure 10*. Experiment 2: Though nonsignificant, time estimates in the reward condition were shorter than in the nonreward condition. Error bars are 1 SD.

Figure 11

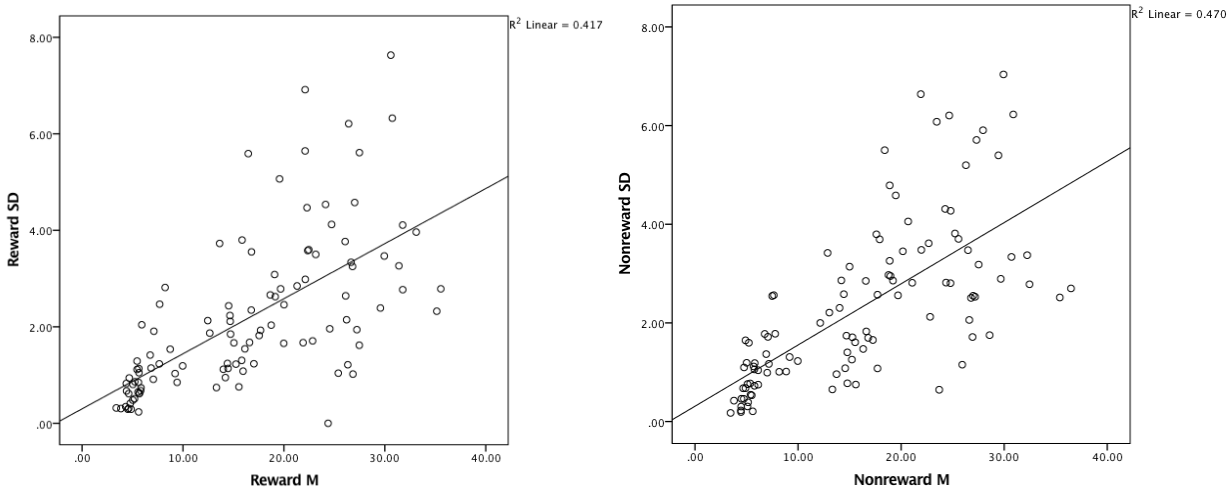


*Figure 11*: Experiment 2. Left: Correlation of means and SDs in the reward condition for all three time durations. The best linear fit is y = 0.30 + 0.11 * x. Right: Correlation of means and SDs in the nonreward condition for all three time durations. The best linear fit is y = 0.31 + 0.12 * x.

Figure 12

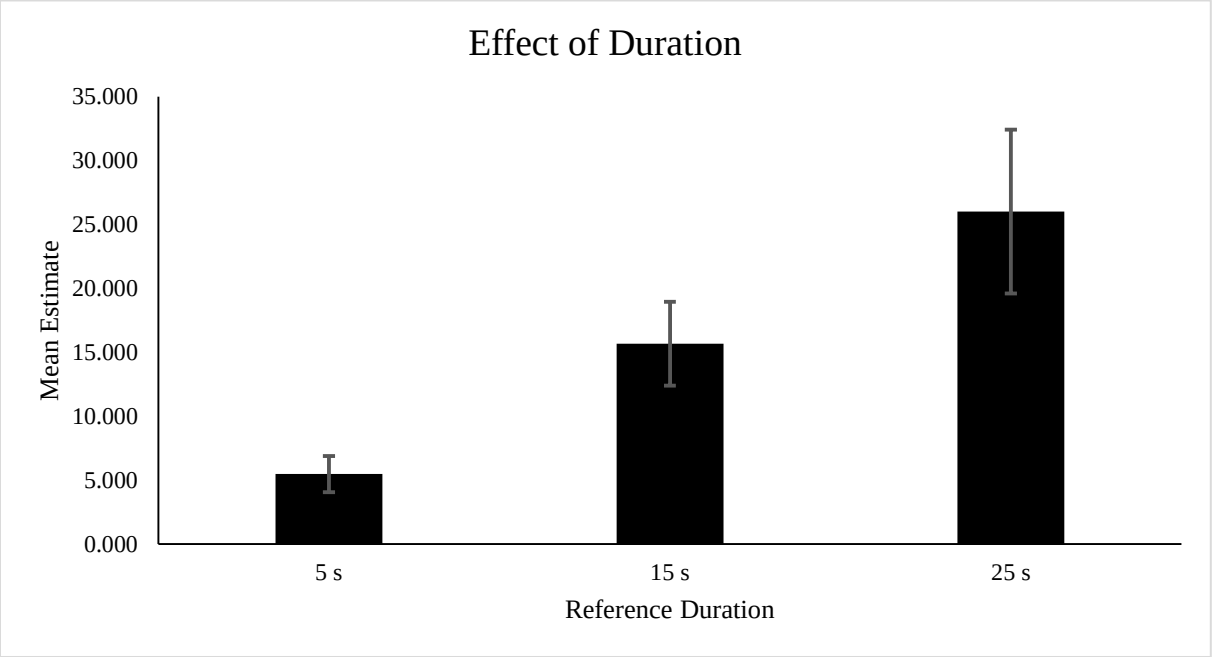


*Figure 12*. Main effect of duration for all participants: For all trials at 5 s in duration, M = 5.47 s, SD = 1.42 s; for all 15 s trials, M = 15.67 s, SD = 3.27 s; for all 25 s trials, M = 26.01 s, SD = 6.40 s. Error bars are 1 SD.

Figure 13

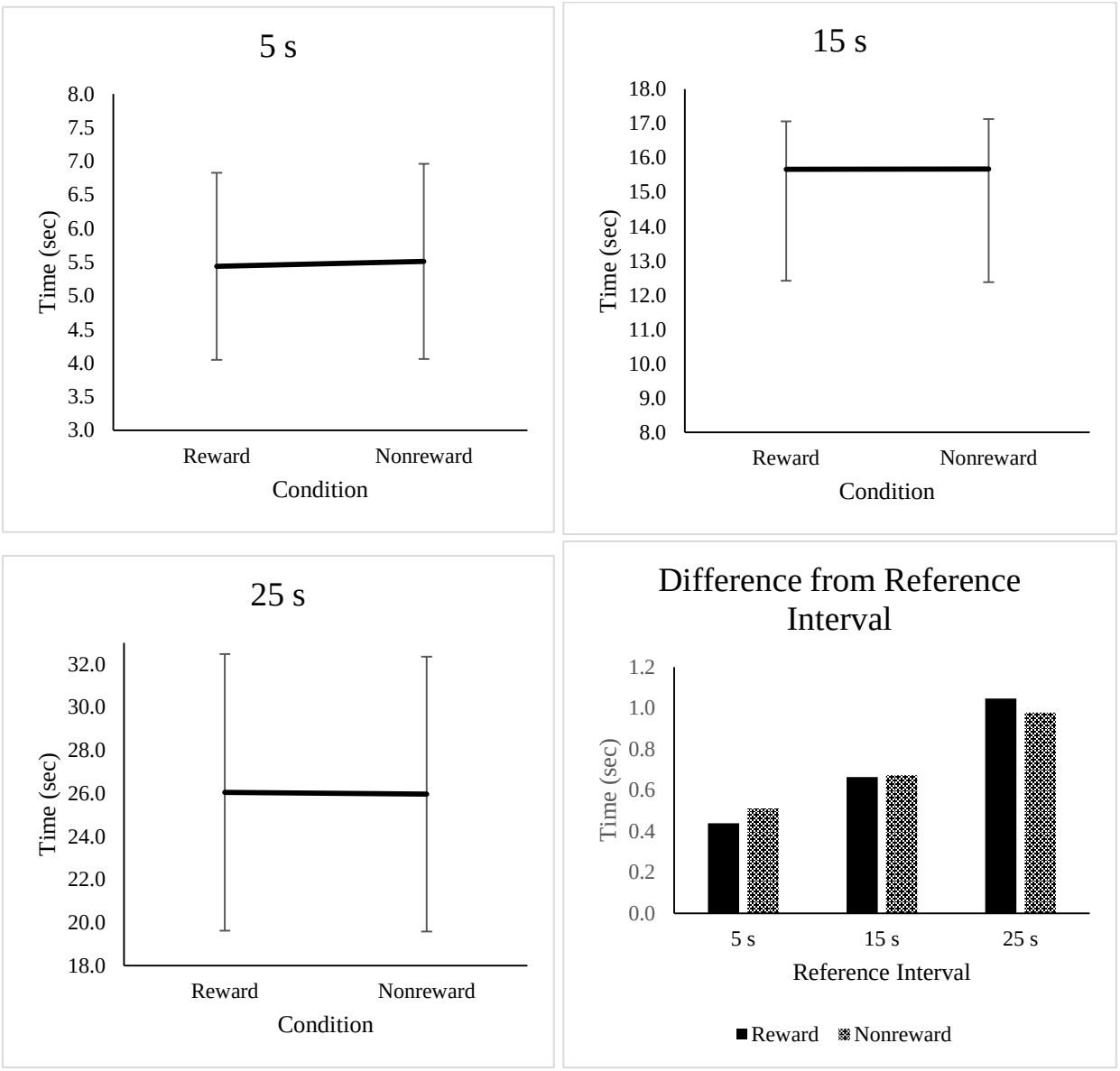


*Figure 13*. All Participants: Though nonsignificant, time estimates in the reward condition were shorter than in the nonreward condition. Error bars are 1 SD.

Figure 14

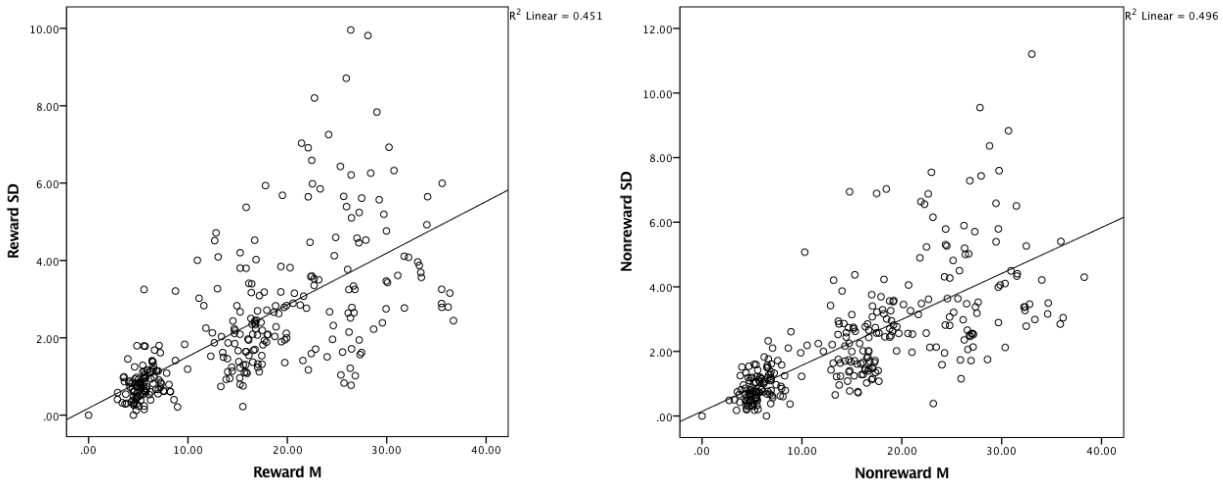


*Figure 14*: All participants. Left: Correlation of means and SDs in the reward condition for all three time durations. The best linear fit is y = 0.18 + 0.13 * x. Right: Correlation of means and SDs in the nonreward condition for all three time durations. The best linear fit is y = 0.14 + 0.14 * x.

Figure 15

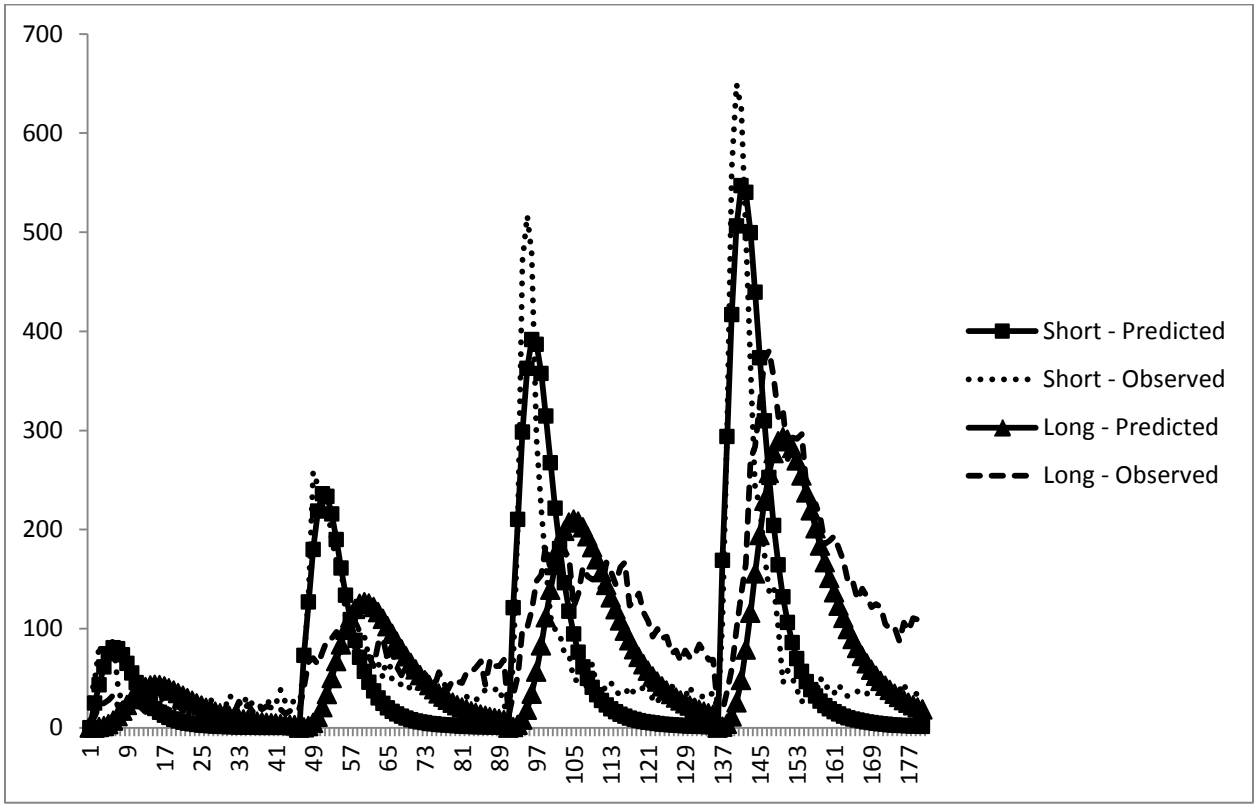


*Figure 15*. Data from Drew et al. (2005) was used to determine the fit of the RTCM model predictions to Drew et al.'s (2005) observed results. Specifically, this experiment measured learning light-shock pairing with either long (15 s) or short (5 s) interstimulus intervals (ISI). Based on the fit of RTCM predictions to the observed data, RTCM appears to explain timed conditioned responses.

Figure 16

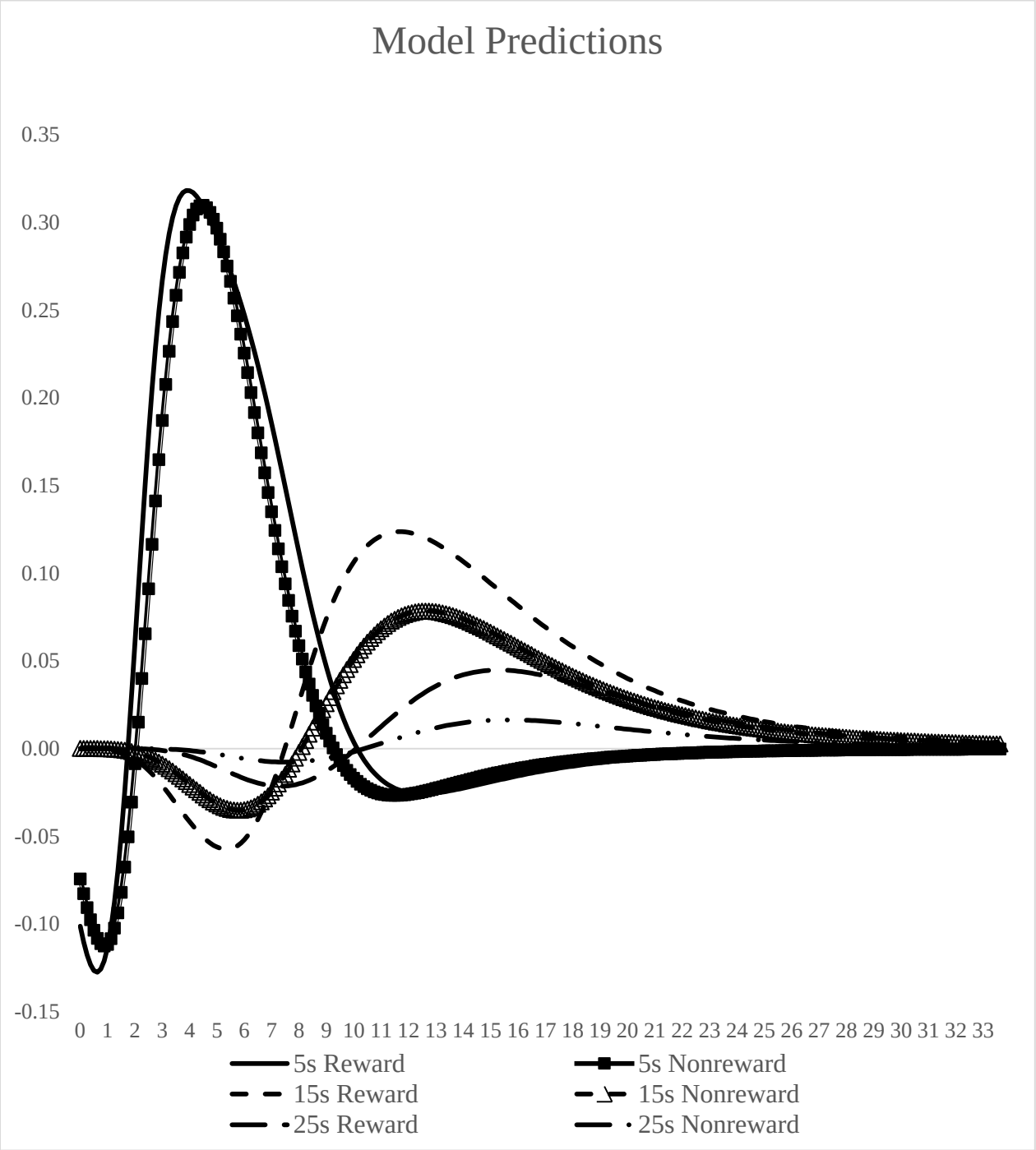


*Figure 16*. RTCM model predictions for the reward and nonreward conditions in the 5, 15, and 25 s time durations. The horizontal axis is time (s); the vertical axis is response strength (-1.0 to 1.0).